Report

Current Biology

Knowledgeable Lemurs Become More Central in Social Networks

Highlights

- We addressed whether learning novel information affects social centrality in lemurs
- Frequently observed lemurs received more affiliation and became more central
- Knowledgeable lemurs whose centrality increased did not initiate more interactions
- There are likely to be feedback dynamics between learning and network position

Authors

Ipek G. Kulahci, Asif A. Ghazanfar,
Daniel I. Rubenstein

Correspondence

ipek.kulahci@gmail.com

In Brief

Social network position influences if and when animals learn from conspecifics. Kulahci et al. show that learning influences network position and that bidirectional relationships exist between the two. Lemurs who learn how to solve a novel task, and solve it while being observed by others, receive more affiliation and become central after learning.

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Current Biology
Report

Knowledgeable Lemurs Become More Central in Social Networks

Ipek G. Kulahci,[1,2,5,*] Asif A. Ghazanfar,[1,3,4] and Daniel I. Rubenstein[1]
[1]Department of Ecology & Evolutionary Biology, Princeton University, Princeton, NJ, USA
[2]Biological, Earth and Environmental Sciences, University College Cork, Ireland
[3]Princeton Neuroscience Institute, Princeton University, Princeton, NJ, USA
[4]Department of Psychology, Princeton University, Princeton, NJ, USA
[5]Lead Contact
*Correspondence: ipek.kulahci@gmail.com

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SUMMARY

Strong relationships exist between social connections and information transmission [1–9], where individuals' network position plays a key role in whether or not they acquire novel information [2, 3, 5, 6]. The relationships between social connections and information acquisition may be bidirectional if learning novel information, in addition to being influenced by it, influences network position. Individuals who acquire information quickly and use it frequently may receive more affiliative behaviors [10, 11] and may thus have a central network position. However, the potential influence of learning on network centrality has not been theoretically or empirically addressed. To bridge this epistemic gap, we investigated whether ring-tailed lemurs' (*Lemur catta*) centrality in affiliation networks changed after they learned how to solve a novel foraging task. Lemurs who had frequently initiated interactions and approached conspecifics before the learning experiment were more likely to observe and learn the task solution. Comparing social networks before and after the learning experiment revealed that the frequently observed lemurs received more affiliative behaviors than they did before—they became more central after the experiment. This change persisted even after the task was removed and was not caused by the observed lemurs initiating more affiliative behaviors. Consequently, quantifying received and initiated interactions separately provides unique insights into the relationships between learning and centrality. While the factors that influence network position are not fully understood, our results suggest that individual differences in learning and becoming successful can play a major role in social centrality, especially when learning from others is advantageous.

RESULTS

Network connections predict individual variation in learning, including learning about the location of novel resources [1–4], the solution of a novel task [5–7], and foraging techniques [8, 9]. Some individuals have higher network centrality than others, either because they are highly connected and have diverse and/or frequent connections or because they occupy key network positions by connecting the otherwise unconnected conspecifics [12, 13]. Central individuals have better access to novel information than non-central individuals [2, 3, 5, 6]. However, beyond age, sex, personality, and developmental stress [13–20], the factors that determine individual variation in social centrality are not fully understood.

Here, we address the possibility that learning influences social centrality. When some individuals acquire novel information before others do, such variation leads to an unequal distribution of information within a group, where some individuals have knowledge that others do not have. This provides opportunities for the naive individuals to observe and learn from the informed conspecifics' behavior. Informed conspecifics may receive more affiliative behaviors and thus become central after they acquire and repeatedly use information. As a result, there may be feedback dynamics between social centrality and information acquisition, where network position is influenced by learning in addition to influencing it.

To test if network position is influenced by learning, we compared individuals' centrality before and after a foraging experiment in two free-ranging lemur groups. Strong social associations and affiliative behaviors play a major role in determining the patterns of selective observation and information transmission [6, 21, 22]. Consequently, we collected data on two affiliative behaviors: approaching another individual to initiate close physical proximity and grooming. We then presented each group with a foraging task that could be solved by pulling a drawer. The task included a single food item (grape) to reduce the likelihood of scrounging so that only the solver, but not the rest of the group, obtained the reward. We first determined if socially central individuals were more likely to learn the task solution after observing others and then asked whether individuals' centrality changed after they learned the task solution. We predicted that the lemurs who learn the task solution sooner than others and solve it frequently while others are observing will receive more affiliative behaviors after the experiment than they did before and thus have higher social centrality.

All lemurs in both groups (Windmill n = 17, Yankee Bridge n = 21) had multiple opportunities to contact the task (mean ± SE = 11.83 ± 2.3 contacts with the task). The first lemurs to solve the task in each group were juveniles (one male in

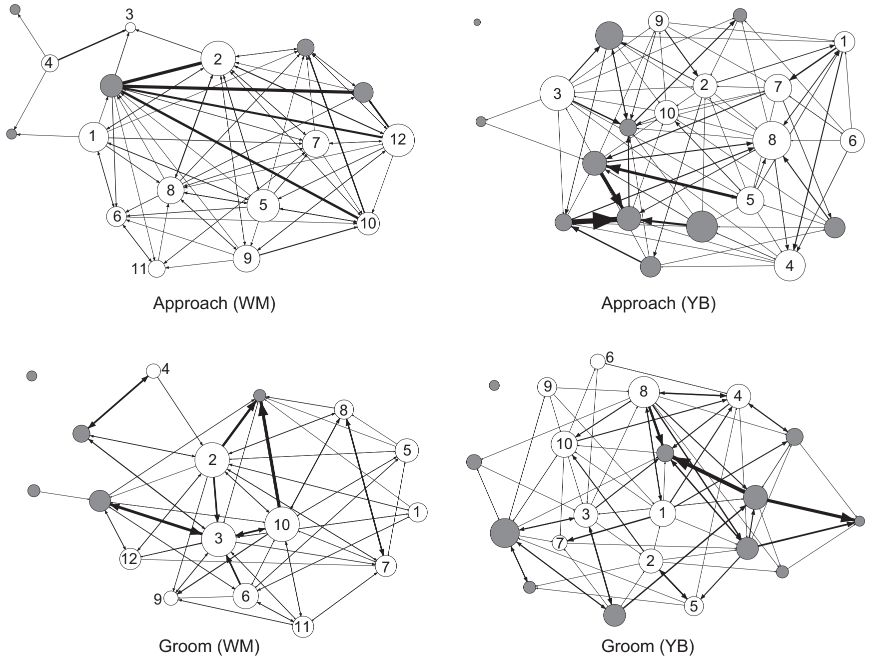

Figure 1. Central Lemurs Are More Likely to Learn the Task Solution

The lemurs who learned (white) were highly social and had engaged in more affiliative interactions than the lemurs who did not learn (gray). Node size: outdegree; numbers: order of learning. Networks are constructed from data collected before the task learning experiment.
See also Table S1.

Windmill, one female in Yankee Bridge). The rest of the group members observed at least one conspecifics' task solving behavior before solving the task for the first time themselves (excluding the initial solvers in each group, frequency of observing an informed conspecific before solving for the first time mean ± SE = 17.38 ± 3.8 observations; number of informed conspecifics observed before solving mean ± SE = 2.81 ± 0.4 individuals). Across both groups, 22 lemurs solved the task, and some solved it more frequently than others (n = 12 in Windmill; n = 10 in Yankee Bridge; task solving frequency mean ± SE = 32.77 ± 12.3; Table S1). Observing conspecifics interact with the task increased lemurs' interest in it, complementing a pattern that has previously been documented in meerkats [23], squirrel monkeys [5], and ravens [6].

Socially Central Lemurs Are More Likely to Learn after Observing

Individuals with high centrality in proximity and affiliation networks are more likely than others to socially learn novel information, potentially because being connected provides more opportunities for selectively attending to, and learning from, the conspecifics who tolerate them in close proximity [5, 6, 21]. To determine whether individual variation in social centrality influenced learning, we used network data that was collected before task presentation and calculated two centrality measures, including "degree," the number of connections, and "strength," the frequency of connections [13, 19, 24]. We distinguished between "indegree" (number of conspecifics from whom an individual receives an interaction) and "outdegree" (number of conspecifics toward whom an individual initiates an interaction). "Outstrength" and "instrength" were defined similarly to indegree and outdegree but included information on the frequency of interactions.

Consistent with previous studies on information transmission [2, 3, 5, 6], we detected positive relationships between individuals' network centrality and whether they acquired novel information. When we excluded the first solver in each group, we found that the lemurs who had initiated more affiliative behaviors were more likely to learn the task solution (Figure 1). Approach outdegree, in particular, predicted learning (Windmill: F = 8.71, p = 0.013, n = 17; Yankee Bridge: F = 8.339, p = 0.01, n = 21). Neither sex nor age (adult or juvenile) influenced whether lemurs learned the task solution (Logistic regression: X^2 = 4.708, p = 0.095; effect of sex: X^2 = 0.745, p = 0.388, effect of age: X^2 = 3.428, p = 0.064).

Frequently Observed Lemurs Become More Central in Affiliation Networks

In each group, the first solver solved the task most frequently (Table S1). There was a positive correlation between solving the task sooner than others and solving it frequently (data from both groups, $F_{1,21}$ = 11.565, p = 0.003; data from individual groups, Windmill: $F_{1,11}$ = 14.539, p = 0.003, n = 17, Yankee Bridge: $F_{1,9}$ = 7.41, p = 0.026, n = 21). However, the frequency of solving the task, but not learning it sooner, predicted how frequently each solver was observed by naive conspecifics (frequency of solving: Windmill: F = 477.351, p < 0.001, n = 17; Yankee Bridge: F = 506.919, p < 0.001, n = 21; order of solving: Windmill: F = 0.454, p = 0.517, n = 17; Yankee Bridge: F = 0.006, p = 0.939, n = 21).

To address whether social centrality increased after being observed while using novel information, we compared individuals' centrality measures before and after the task learning experiment. Because we were interested in the change in centrality rather than in its raw values, we ranked each individual's centrality measures relative to their group members' measures. We included both the initial solvers and the lemurs who learned after observing in this analysis. We predicted that if the frequently observed lemurs receive more affiliative behaviors after learning than they did before, then this change would be detected as an increase in indegree and instrength. We also predicted that frequently observed lemurs' outdegree and outstrength would remain the same. Out-measures indicate the behaviors that are initiated and are thus more likely to reflect the degree to which individuals are social (e.g., their social personality traits [14, 25]).

Comparing centrality ranks before and after the learning experiment revealed that the frequently observed lemurs had higher centrality (indegree and instrength) after the experiment

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Table 1. The Frequency of Being Observed Predicts the Increase in Social Centrality

Centrality measure	f value	p value
Approach Indegree*	5.197*	0.036*
Approach Instrength*	5.647*	0.033*
Approach Outdegree	0.874	0.370
Approach Outstrength	0.2	0.662
Groom Indegree*	8.487*	0.012*
Groom Instrength*	4.788*	0.047*
Groom Outdegree	0.238	0.631
Groom Outstrength	1.512	0.239

The frequently observed lemurs had higher indegree and instrength after the experiment than they did before, while their outdegree and outstrength did not change. The p values are generated from a permutation-based node-level regression test. Significant changes are indicated with an asterisk.

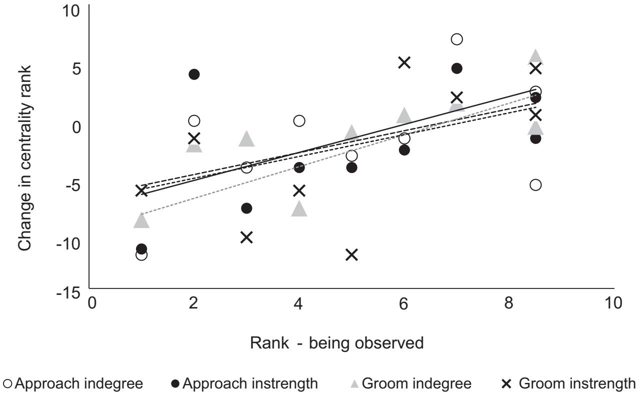

Figure 2. Frequently Observed Lemurs Become More Central in Affiliation Networks

Data shown from the frequently observed lemurs in Windmill (n = 17). Because of high inter-individual variation in the frequency of being observed, we plotted ranks instead of raw values. The most frequently observed lemur was assigned a rank of 1 (x axis). A negative change in centrality rank (y axis) indicates that the lemur became more central after the experiment.

See also Table S1.

than they did before the experiment (Table 1). This increase was correlated with the frequency of being observed and was detected only for the frequently observed lemurs, but not for the other lemurs who solved the task (Figure 2). Notably, receiving more affiliative behaviors, and the corresponding increase in indegree and instrength, was not due to initiating more affiliative behaviors toward others, as indicated by the lack of change in outdegree and outstrength (Table 1). In addition, an increase in received interactions did not result in an increase in interactions that were given to others. Solving the task frequently while being observed was essential for receiving more affiliative behaviors and becoming more socially central after the experiment.

DISCUSSION

Some species, including primates, form long-term differentiated social bonds that are maintained through affiliative behaviors [26–28]. However, the motivating factors and the underlying mechanisms behind these bonds are not yet fully understood. Our study suggests that individual differences in learning and using novel information may influence who bonds with whom. Individuals who quickly and accurately acquire information and use this information frequently may be perceived as reliable information sources or as successful individuals (e.g., successful foragers, mates, group leaders, or cooperation partners). Being socially connected to successful and knowledgeable individuals would be advantageous for future social learning opportunities, as animals tend to observe and learn from those with whom they share affiliative connections [6, 21, 22].

When solving a task leads to the availability of multiple food items such that individuals other than the solvers can also obtain food [10, 11], individuals may associate or affiliate with the solvers for increased tolerance and scrounging opportunities. Several primate species frequently groom conspecifics who solve a task and provide food to the group [10, 11, 29]; some even adjust their grooming based on how many conspecifics provide such benefits [11]. Our task included only a single food item to reduce scrounging and food sharing, and we detected centrality changes after the task was removed. Furthermore, the lemurs who groomed the frequently observed individuals did not receive more grooming from these individuals. Thus, we detected centrality changes in the absence of immediate benefits such as scrounging and mutual grooming, suggesting that immediate benefits are unlikely to be responsible for knowledgeable individuals' increase in centrality. Instead, our results support the idea that short-term benefits cannot fully explain all the affiliative interactions in animals [26]. Preferentially associating and interacting with knowledgeable and successful conspecifics may provide future and long-term benefits, and this would have long-term consequences for social connections.

So why did the frequently observed lemurs receive more affiliative interactions in the absence of immediate benefits and without initiating more interactions themselves? Although our design does not allow us to distinguish between potential mechanisms responsible for this change, we offer a few potential explanations, some of which may be acting together to influence the patterns we observed. One possibility is that the increased affiliation was due to carry-over effects from the learning experiment. During the experiment, lemurs may have started to affiliate with the conspecifics they observed, and this affiliation may have continued after task removal, especially if observers continued to stay in close proximity and attend to the behaviors of those they observed.

Another possibility is that learning and using novel information successfully influences how individuals are perceived by their conspecifics. Knowledgeable humans are considered "prestigious" and receive social benefits [30]. Although social rank is assumed to be similar to prestige [31] and some species preferentially learn from older or dominant individuals [32, 33], dominant females in our study did not have high centrality, nor did they solve the task (Table S1). Thus, gaining information about the environment and contributing to group knowledge [34] may be more important than dominance in determining who becomes influential and receives affiliation. Because factors including rank, age, sex, and personality influence variation in learning [21, 35–37] and in social centrality [13–20], carefully designed experiments are needed to uncouple their effects on the relationships between learning and centrality. One promising method involves manipulating the identity of the knowledgeable individuals, either through selective access experiments that use automated or remote controlled devices [11] or through training specific individuals on complicated tasks [10]. For example, low-ranking primates who are presented as the only task-solvers and food-providers receive frequent affiliation from others [10, 11]. A particularly exciting manipulation would involve choosing individuals based on their learning ability. Explorative individuals tend to be innovative and learn novel information faster [38, 39] and, in some species, also have high centrality [20]. If a non-central individual, who is neither explorative nor innovative, is presented as the only knowledgeable individual and becomes central after being observed, this would suggest that the centrality increase is due to conspecifics' social responses to that individual's repeated use of information.

It is also possible that the frequently observed lemurs were perceived as successful foragers. We cannot directly distinguish whether the increase in frequently observed lemurs' centrality was due to their task learning ability, resulting in them being perceived as successful solvers, or their ability to repeatedly gain food, resulting in them being perceived as successful foragers. Cognitive abilities, such as learning ability, cannot be quantified directly but are instead inferred from their influence on behavior [36, 40]. Individuals who successfully learn about novel food and use this information while foraging are likely to become successful foragers and may receive increased attention and affiliation from conspecifics. To determine whether the changes in centrality are due to the ability to solve the task (i.e., learning success) or due to the ability to gain food (i.e., foraging success), additional experiments can be run, by utilizing selective learning tasks that deliver food only to some solvers, but not to the other solvers, or by setting up selective foraging patches at which only some individuals can forage.

Changes in centrality after information transmission can affect the inferences we make about the patterns of transmission through networks. For instance, if we find that central individuals are more likely to learn novel information through social transmission, it is important to rule out the possibility that those individuals became central only after acquiring and using that information. Some options for ruling out this possibility include using network data that was collected before information transmission (as done in our study) or using dynamic social networks to quantify changes in centrality during and after transmission.

Distinguishing between initiated behaviors (quantified by out-measures) and received behaviors (quantified by in-measures) can be highly informative in understanding the patterns of social learning. The centrality changes we detected were based exclusively on in-measures; frequently observed lemurs received more affiliative behaviors without initiating more affiliative behaviors themselves. If naive individuals preferentially initiate interactions toward knowledgeable individuals, then out-measures may be more informative than in-measures at predicting who learns novel information when. To our knowledge, this possibility has not yet been empirically incorporated into social learning and transmission studies.

Conclusion

We demonstrate that the relationships between social network centrality and learning are bidirectional and based on feedback dynamics, such that in addition to centrality influencing who learns novel information and when they learn it, learning and using novel information influences centrality, as well. Individual differences in learning about the environment will lead to individual differences in success at utilizing resources and can thus play an important role in centrality, and ultimately in social structure, by influencing social behaviors toward the knowledgeable conspecifics. We strongly encourage studies that investigate the dynamic nature of centrality and the potential ways in which it can be influenced by individual differences in acquiring and using novel information.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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    - Task presentation
- QUANTIFICATION AND STATISTICAL ANALYSIS
- DATA AND SOFTWARE AVAILABILITY

SUPPLEMENTAL INFORMATION

Supplemental Information includes one table and can be found with this article online at https://doi.org/10.1016/j.cub.2018.02.079.

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AUTHOR CONTRIBUTIONS

Conceptualization: I.G.K. Methodology: I.G.K., A.A.G., D.I.R. Investigation: I.G.K. Formal Analysis: I.G.K. Writing- Original Draft: I.G.K. Writing- Review & Editing: I.G.K., A.A.G., D.I.R.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Mendeley Data	This paper	https://doi.org/10.17632/3h6cg9z87c.1
Experimental Models: Organisms/Strains		
Lemur catta	St. Catherine's Island, Georgia, United States	N/A
Software and Algorithms		
UCINET	Analytic Technologies (http://www.analytictech.com/archive/ucinet.htm)	version 6.647

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Ipek G. Kulahci (ipek.kulahci@gmail.com).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

We worked with two groups of free-ranging ring-tailed lemurs (*Lemur catta*) at the St. Catherine's Island (GA, USA). The first group (Yankee Bridge n = 21; 8 females, 13 males; 12 juveniles, 9 adults) was studied June-August 2012, while the second group (Windmill n = 17; 7 females, 10 males; 7 juveniles, 10 adults) was studied July through October 2013 (Table S1). Lemurs were individually identifiable through facial variation, visual features, collars, and tail shaves. All lemurs were habituated to the experimenter (IGK), allowing observations and task presentation to take place without disturbing their behavior. All procedures were approved by the Institutional Animal Care and Use Committee at Princeton University (Protocol # 1868).

METHOD DETAILS

Network data

We used all occurrence sampling to collect social interaction data on two affiliative behaviors: approaching a conspecific to initiate close physical proximity and grooming. Groups were observed before and after, but not during, the task experiment (number of observation hours: Windmill before experiment = 48 hr, after experiment = 45 hr; Yankee Bridge before experiment = 54 hr, after experiment = 51 hr). We recorded similar number of interactions before and after the experiment (Windmill approach: 220 interactions before, 230 interactions after; Windmill groom: 210 interactions before, 233 interactions after; Yankee Bridge approach: 173 interactions before, 135 interactions after; Yankee Bridge groom: 146 interactions before, 151 interactions after). Social interaction data were converted into network matrices and analyzed in UCINET (version 6.647) [41]. Social data were collected outside of the task experiment to avoid potential influences of the task and the reward on who initiated social behaviors toward whom and how frequently.

In approach networks, the lemur who approached a conspecific and sat in close physical proximity (within one body width or closer) was the actor of the interaction. The lemur who was approached was the receiver of the interaction. Approach networks included only the instances that did not result in another interaction, allowing us to prevent including the same data in multiple networks. For instance, if a lemur approached a conspecific and started grooming her, then this interaction was only entered into the grooming network but not into the approach network. In grooming networks, the lemur who groomed another was the actor of the interaction, while the lemur who was groomed was the recipient. Lemurs engage in both directed grooming (one lemur grooms another) and mutual grooming (two lemurs groom each other) [14, 42]. Mutual grooming data were converted into directed grooming data by including both of the participating lemurs as the actor and the receiver.

Task presentation

The foraging task was a transparent Plexiglas box (20x20x20cm) that included a single grape to minimize scrounging. Each group was presented with a single box. All lemurs were free to participate in the experiment by approaching and contacting the box during each of the sessions, and we did not exclude any lemurs from the task-learning experiment. Multiple sessions were run on each day. The session lengths varied based on group movement, weather conditions, short-term environmental disturbances, and changes in lemurs' motivation. A session began when a lemur approached the box and ended when no lemurs were within a 1 m radius of the box for 3 min. Each session had multiple trials. Trials ended when the grape was taken. All sessions were recorded with an HD camcorder

(Panasonic HC-V700) placed on a tripod at the same height as the task. The videos were scored for i) who solved the task, ii) the latency of the first solution for each lemur, iii) frequency of solving, and iv) who observed whose solving behavior. Only the lemurs facing the box within a 2 m radius as the box was being opened were counted as observers, to ensure that all the lemurs who were classified as observers had a clear view of the task solution.

QUANTIFICATION AND STATISTICAL ANALYSIS

We used the permutation-based node-level regression test in UCINET (version 6.647) [41] to analyze whether lemurs with high social centrality were more likely than others to learn the task solution (we ran 10000 permutations). For this analysis, we excluded the first solver in each group, as we were interested in how social centrality influenced the likelihood of observing and learning information that was already present in the group. Data from two groups were analyzed separately. We used logistic regression to determine whether sex or age (adult versus juvenile) influenced learning.

To determine which factor predicted the frequency of being observed by naive conspecifics, we entered both the frequency of solving and the temporal order of learning into a model, together with the frequency of being observed (dependent variable). To analyze the relationships between the change in centrality ranks (dependent variable) and the frequency of being observed (rank; independent variable) (Table 1), we used the node-level regression in UCINET (version 6.647) [41]. This regression procedure combines targeted hypothesis testing with randomization tests to deal with the non-independence of network data, by repeatedly permuting the dependent variable (centrality measures) to calculate the p values [43]. We ran 10,000 permutations.

DATA AND SOFTWARE AVAILABILITY

The data used in the analyses reported in this paper are available at Mendeley Data at https://doi.org/10.17632/3h6cg9z87c.1.

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Supplemental Information

Knowledgeable Lemurs Become More Central in Social Networks

Ipek G. Kulahci, Asif A. Ghazanfar, and Daniel I. Rubenstein

ID	Group	Sex	Learned (1); not learned (0)	Solving frequency	Frequency of being observed (rank)
Sycamore	WM	Male	1	250	1
Polli	WM	Female	1	132	2
Poseidon	WM	Male	1	53	3
Waylon	WM	Male	1	67	4
Pigpen	WM	Male	1	28	5
Alder	WM	Male	1	24	6
Rachel	WM	Female	1	9	7
Autumn	WM	Female	1	7	8.5
Willie	WM	Male	1	2	8.5
Birch	WM	Male	1	1	
Charlie	WM	Male	1	1	
Dolly	WM	Female	1	1	
Cakid	WM	Female	0		
Chagall	WM	Female	0		
Cy	WM	Male	0		
Diego	WM	Male	0		
Jen (*)	WM	Female	0		

ID	Group	Sex	Learned (1); not learned (0)	Solving frequency	Frequency of being observed (rank)
Orion	YB	Female	1	49	1
Poseidon	YB	Male	1	43	2
Zeus	YB	Male	1	25	3
Annie	YB	Female	1	10	4
Hickory	YB	Male	1	7	5
Cypress	YB	Male	1	7	6
Mary	YB	Female	1	2	7
Chaos	YB	Male	1	1	8.5
Remington	YB	Male	1	1	8.5
Buffalo	YB	Male	1	1	
Austin	YB	Male	0		
Cy	YB	Male	0		
Diego	YB	Male	0		
Lillie	YB	Female	0		
Magda	YB	Female	0		
Marla	YB	Female	0		
Nikki (*)	YB	Female	0		
Pinus	YB	Male	0		
Redbay	YB	Male	0		
Rockwell	YB	Male	0		
Tupelo	YB	Female	0		

Table S1. Data on frequency of task solving and being observed, related to Figures 1 and 2.

Data from two lemur groups Windmill WM (n=17) and Yankee Bridge YB (n=21). Dominant females are indicated with an asterisk.