Large group and moderate cognitive abilities favor the evolution of badges of status over individual recognition

Eleanor Brush[1] and Elizabeth A. Hobson[2,3,4]

[1] Department of Biology, University of Maryland, 4094 Campus Dr., College Park, MD 20742; email: eleanor.brush@gmail.com
[2] Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501 USA
[3] Center for Biosocial Complex Systems, Arizona State University
[4] National Institute for Mathematical and Biological Synthesis, University of Tennessee, Knoxville, TN, USA; email: ehobson@santafe.edu

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2   **Abstract**

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5

6   **Introduction**

7   1. why signals and recognition and assessment are interesting and important

8   2. two solutions

9   3. what we know about how badge systems might have evolved

10   • honest signaling

11   4. what we know about how individual recognition systems might have evolved

12   • Dunbar's number

13   5. Little work has been done to explicitly compare the two systems and identify the types of
14   species or social groups in which one or the other would be more likely to evolve, a deficit
15   highlighted by [9]

16   6. approach

17   7. questions

Animals in social groups benefit from having accurate information about their group mates. For example, knowing about the dominance XXX, resource holding potential XXX, likelihood of investing in parental care XXX, or health XXX of other animals can help an animal decide with whom to fight, mate, or interact. In order to learn about one's group mates, an animal must be able to identify them. There are many solutions to this problem. Some animals can recognize other members of their groups as individuals. Other animal coarsely categorize conspecifics based on traits they exhibit. When such a trait is correlated with another property of interest, for example dominance or health, it becomes a badge of status, which allows animals to make inferences about each others' quality as mates or opponents or allies XXX. Much is known about what circumstances might promote the evolution of one or the other type of learning XXX, but there are few studies that compare the two systems directly [9]. In this paper, we develop and analyze a simple model of an animal social group, in which animals learn by interacting with each other and by observing these interactions, in order to learn how group size and cognitive abilities affect the effectiveness of using both types of learning and to determine the circumstances under which one or the other is preferable.

There are many species in which animals have been shown to use badges of status to make inferences about each other. One well known-example is the house sparrow (XX): the size of a male sparrow's black bib is correlated with its physical condition and other sparrows seem to use this information to decide how to interact with a given male XXX. Another well-studied example is the paper wasp (XX): the extent of black and the number of black patches on a wasp's face are positively correlated with its dominance, suggesting that wasps use that trait when deciding with whom to fight and how aggressively [11]XXX. Other examples include XXX. It has been shown that XXX factors promote the evolution of a badge that is correlated with quality. When a group starts to use a badge as a proxy for quality, an incentive appears for low-quality animals to "cheat" and produce a badge that indicates they are higher quality than they actually are. This would seem to lead to the loss of an informative signal. One mechanism that can keep a badge "honest" is the cost required to produce or maintain it XXX. However, even cost-free signals can maintain their honesty XXX. We focus here on the factors that might lead to the evolution of learning system that relies on badges, rather than the evolution of the badges themselves, since the former has received relatively little attention.

There are also many animals that can individually recognize their group mates. These include XXX

While badges of status and individual recognition are usually presented as fundamentally different solutions to the same biological problem, individual recognition is in some ways just an extreme version of learning about others' badges [1]. Animals that make inferences about their peers based on the badges they display are limited by their perceptive and cognitive abilities: if two

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animals have badges that are close enough in size that others cannot tell the difference between them, their peers will judge that they have the same size badge and therefore the same "quality." As perceptive abilities improve, an animal will be able to make finer distinctions about its peers, to the point that it may be able to recognize each of them individually. (We use vision here for the sake of clarity, but the same holds true for other senses as well.) Such a spectrum from coarse-grained to fine-grained perceptive abilities can be seen in the group of paper wasp species. In some species, wasps distinguish between other wasps based on the number of black patches on their face, a relatively coarse trait [11]XXX, whereas in some species wasps can recognize other individuals based on their unique facial patterns XXX. The correlation between the badge and another trait has received a lot of attention in previous studies of the evolution of badges of status. However, the specificity with which the badge can be perceived has not been. As we show below, it is a crucial factor in determining how effectively an animal can learn from its group mates' badges.

Many factors. Recent work ([9]) provides several predictions but focused on predicting differences in signaling systems comparing an innate quality signal to a social recognition system across different species, not within species ([8]).

Our goal is to better understand how learning the quality of conspecifics is affected by differences in group size, memory, and perceptive ability. We also want to determine the conditions under which the evolution of a badge signal or individual recognition would be favored. We simulated quality assessment through interactions among individuals. Each time individuals interact, they are able to assess each other's quality and update their previous opinion about quality. We use two quality assessment methods: (1) Badge signal systems: individuals group others into quality categories based on the intensity of badge signals and (2) Recognition systems: individuals use individual recognition to remember the outcome of events with particular individuals to estimate quality.

Model

Each animal in the social group has an inherent quality value. This can be thought of, for example, as fighting ability [], resource holding potential [], body size, body condition, or any other property about which it would be beneficial to have information. In our basic model, an animal learns about another's quality value by interacting with it directly. We also extend our model to cases where animals can learn through observing the interactions between other pairs in addition to direct interactions. We consider two different methods of learning: individual recognition and badges. An animal using individual recognition can identify each of its group mates as a particular individual. An animal using the badge system only recognizes animals based on the signals they display in a categorical fashion. Our model assumes that it is costly to the animals in the group to learn about each other inaccurately. Since animals can use information about their group mates to decide how to interact with them in the future, having the wrong information can lead to an inappropriate choice. We also assume that it is also costly to learn slowly. The time spent interacting and learning about one's group mates could be spent in other ways. Additionally, if the interaction is actually a fight between animals, having more interactions than necessary can lead to injury and perhaps even death. Finally, we also assume that having improved memory and perceptive ability is costly because of the associated energetic costs of larger brain or because improving

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these properties involves a trade-off that negatively affects other traits. We combine the costs associated with inaccurate learning, the time required to learn, and cognitive abilities to assess the performance of animals using each of the two learning systems.

Interactions and learning

We assign each animal a quality value, q_i, and a signal, s_i, which is always perceptible to conspecifics. We define the parameter ρ as the correlation between the signals, $\{s_i\}$, and the quality values, $\{q_i\}$. In a group with N animals, we draw quality values $\{q_1, \ldots, q_N\}$ from a normal distribution with mean 0 and standard deviation σ_{q}. We then generate N signal values such that $\min_i s_i \approx -1$, $\max_i s_i \approx 1$, and the correlation between $\{q_i\}$ and $\{s_i\}$ is precisely ρ. (A list of the variables used in the text is provided in Table 1.) The question of how a signal comes to be correlated with quality is an interesting one. Some of the circumstances that can allow for this to happen include XXX In the future, we plan to include an evolutionary timescale in our model and to consider the evolution of the signal, but for the moment, we assume the signal-quality correlation is fixed at a given level. We do not consider or allow for cheating in this model (i.e. lower-quality individuals cannot display a higher than expected signal intensity, all individuals display signals that are linked to their underlying quality in the same way).

Each animal assesses the quality of each other animal: $a_{ij}(t)$ is the opinion of animal i about animal j at time t. At first, the group consists entirely of naive animals: at $t = 0$, no animal has an opinion of any other. Every animal has a memory window of length w. At each point in time, first, if animal k has not updated its opinion of animal ℓ within the last w timesteps, it forgets its opinion of ℓ. Next, two animals, i and j, are chosen randomly to interact. If i already has an opinion of j, its updated opinion is

$$a_{ij}(t) = (1 - \ell_{\mathsf{i}})a_{ij}(t-1) + \ell_{\mathsf{i}}q_j + \xi,$$

where ℓ_{i} is a parameter describing how much i changes its opinion based on the interaction and ξ is drawn from a normal distribution with mean 0 and standard deviation σ_{i}. If i and j have not previously interacted or i has forgotten its opinion of j, then after interacting

$$a_{ij}(t+1) = (1 - r)b_i(t) + rq_j + \xi,$$

where $b_i(t)$ is a baseline opinion of any animal it encounters. Specifically, $b_i(t)$ is drawn from a normal distribution with mean 0 (the expected quality value of any animal) and standard deviation σ_{b}. The other animals in the group observe the interaction with probability p_{o}. If animal k observes the interaction, it uses the same rules to update its opinion of both i and j, with parameters ℓ_{o} and σ_{o}. We use $\ell_{\mathsf{o}} \leq \ell_{\mathsf{i}}$ and $\sigma_{\mathsf{o}} \geq \sigma_{\mathsf{i}}$ so that observational learning is noisier. This completes the description of how learning occurs for animals using individual recognition.

Badge system

An animal that uses the pure badge system to learn cannot perceive the difference between animals with similar signals and is forced to make a noisy estimate of the quality values of all such animals. Specifically, an animal divides the rest of its group into categories before any interactions take place. It does so by picking another animal, j, at random. All animals whose signals are

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within $\delta/2$ of s_j are put in the same category. Then the focal animal picks an uncategorized animal at random, k, forming a second category of all uncategorized animals whose signals are within $\delta/2$ of s_k. The process continues until every animal in the group has been assigned a category. Category width δ depends on the animals' perceptive abilities. For example, if δ is large, an animal might only be able to identify animals with small, medium, and large signals, whereas if $\delta = 0$ an animal can identify every individual in its group and using the badge is no different than using individual recognition. Different animals will categorize the group differently and may perceive different numbers of categories. Figure S1 shows one example of this process. The average number of categories animals perceive decreases with group size and category width, δ (Figure S2). When an animal using the badge system updates its opinion of another animal based on direct interaction or on observation, it simultaneously updates its opinions of all the other animals in the same category. If an animal observes an interaction between two animals in the same category, it does not updates its opinion of that category.

Measures of performance

The animals interact and learn about each other for T timesteps. To measure each animal's learning ability, we average the errors it makes in its opinions about the rest of the group:

$$\epsilon_i(T) = \frac{1}{|\mathscr{O}_i(T)|} \sum_{j \in \mathscr{O}_i(T)} |a_{ij}(T) - q_j|,$$

where $\mathscr{O}_i(T)$ is the set of animals about whom i has an opinion at time T. We also calculate the average time it takes for an animal's error about each other animal to drop below a threshold:

$$\tau_i = \frac{1}{|\mathscr{O}_i|} \sum_{j \in \mathscr{O}_i} \min_{t=1,\ldots,T} \{t : \epsilon_{ij}(t) \le 0.2\}.$$

(If ϵ_{ij} is always greater than the threshold, then i's learning time about j is taken to be T.) Figure S3 shows one example of this calculation. We model 25 groups of animals using each of the two learning systems and calculate the average error $\bar{\epsilon}$ and average learning time $\bar{\tau}$ of all animals in all groups. In Figure **??** we show how the average error of animals using each of the two systems changes over time.

Learning errors and learning time can both be costly. Individuals can gain long-term benefits from assessing each others' quality. Improving perceptive ability (by decreasing δ) and improving memory (by increasing w) can also be costly XXX.

We describe the cost of the category width with the function

$$c_\delta = \left(\frac{2-\delta}{2}\right)^\alpha$$

and that of memory with the function

$$c_w = \left(\frac{w}{2000}\right)^\alpha,$$

where α is a parameter determining the concavity of the cost function. The animals pay no costs for having no cognitive ability ($\delta = 2$ and $w = 0$), and 1 unit of cost for optimal cognitive ability ($\delta = 0$ and $w = 2000$, the highest w we consider). (Figure S4 shows these cost functions.) We then combine the four sources of cost—error, time, memory window, and category width—into the total cost

$$C = 2\bar{\epsilon} + 10^{-4}\bar{\tau} + c_w + c_\delta,$$

where the terms in front of $\bar{\epsilon}$ and $\bar{\tau}$ ensure that the four factors, $\bar{\epsilon}$, $\bar{\tau}$, c_w and c_δ, are on the same scale.

Table 1: Description of variables

Variables	Description of variables
C	total cost of learning
δ	category width
ϵ_i	average error of animal i about all other animals
$\bar{\epsilon}$	average error of all animals in all groups
ℓ_i	learning rate in direct interaction
ℓ_o	learning rate in indirect observation
N	number of animals in group
p_o	probability of observing interactions between other pairs
q_i	quality of animal i
ρ	correlation between quality and signal
s_i	signal of quality / badge of status of animal i
σ_b	standard deviation of baseline opinion
σ_i	standard deviation of noise in opinion updating during interaction
σ_o	standard deviation of noise in opinion updating during observation
σ_q	standard deviation of quality values
T	total number of fights
τ_i	average learning time of animal i
$\bar{\tau}$	average learning time of all animals in all groups
w	memory window

Results

The effects of group size and cognitive abilities on learning

We first analyze the model without any observational learning ($p_o = 0$). We compared three parameter combinations to visualize how average error decreases over time (Figure 1). Average errors in quality assessment generally decreased over time until errors stabilized and were no longer affected by the number of interactions. Stabilization of errors is indicative that maximum learning has been reached. In most cases, this maximum learning point was reached much more quickly in the categorical badge system than in the individual recognition system [*hard to tell exactly with panel C, does indiv recog stabilize before badge there?*]. Badges with lower signal
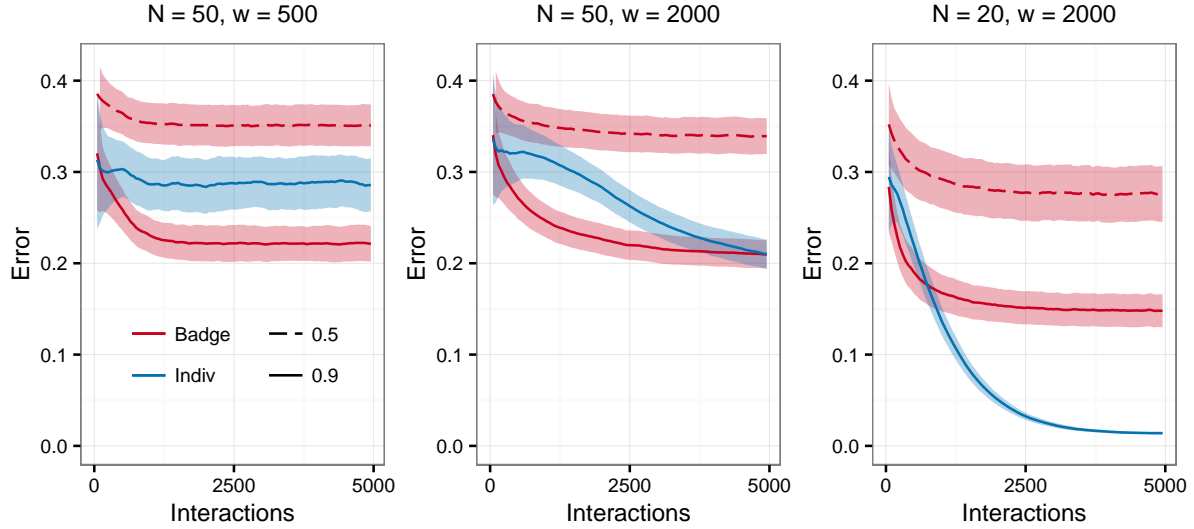
Figure 1: **Examples of how average error decreases over time.** In each panel, we show time in number of interactions on the x-axis and average error, $\bar{\epsilon}$, on the y-axis. The line shows the average error across all animals in all groups and the shaded area shows this average ± 0.5 the standard deviation of error across all animals in all groups. In each panel, blue lines show animals using individual recognition and red lines show animals using the badge system. The solid lines correspond to groups where signal-quality correlation $\rho = 0.9$ and the dotted lines correspond to groups where signal-quality correlation $\rho = 0.5$. As groups size increases, from A to B, the error of animals using both systems increases, but it affects the error of animals using individual recognition more. As memory window decreases, from B to C, the error of animals using the badge system is not strongly affected, whereas the error of animals using individual recognition becomes higher. Parameters: in all panels $\delta = 0.5$, $\ell_i = 0.2$, $p_o = 0$, $\sigma_b = 0.2$, $\sigma_i = 0.01$, $\sigma_q = 0.5$, $T = 10000$; in A $N = 20$, $w = 2000$; in B $N = 50$, $w = 2000$; in C $N = 50$, $w = 500$.

to quality correlation strengths (R=0.5) resulted in the largest errors in quality assessment across all three comparisons (dotted red lines, Figure 1). Individual recognition in small groups (N=20) resulted in the most accurate quality assessments of all comparisons, but required a large number of interactions before this accurate assessment was reached (Figure 1A). In larger groups (N=50), many more interactions were required for the individual recognition systems to become accurate, and assessment did not reach the accuracy seen in small groups. Quality assessment under both badges and individual recognition were less accurate when group size increased, and the accuracy of individual recognition was more affected than in the badge system (Figure 1B). Error rates were even higher when we compared larger groups with a long memory span (Figure 1B) to larger groups with a smaller memory span (Figure 1C). In this case, when we decreased the memory span of individuals, the error in quality assessment in individual recognition increased, and average errors were higher when memory was shorter, although individual recognition still outperformed the badge with lower signal to quality correlation.

The effects of group size N, memory window w, and signal-quality correlation ρ on error and learning time are intuitive and confirm that our model is a reasonable description of a real social system. For animals using both learning systems, smaller groups and longer memory windows make it easier to learn. As group size decreases, both error and learning time decrease (Figure 1A,B; Figure 2A,B). As memory window increases, error decreases and learning time either
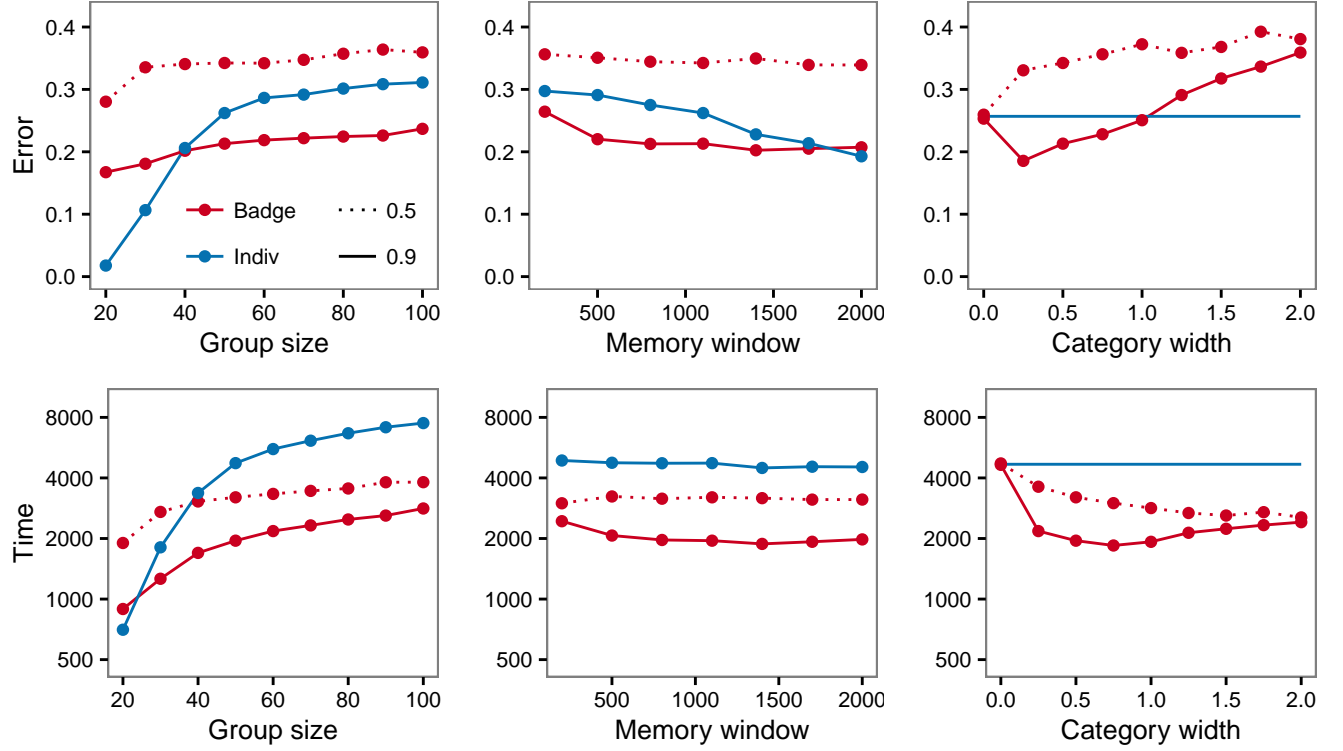
Figure 2: **Decreasing group size and increasing memory window both improve learning in the absence of observation.** Error and learning time are minimized at an intermediate category width. In the left column, we show average error $\bar{\epsilon}$ as a function of various parameters, and in the right column, we show average learning time $\bar{\tau}$ as a function of various parameters. In each panel, blue lines show animals using individual recognition and red lines show animals using the badge system. The solid red lines correspond to groups in which the signal-quality correlation $\rho = 0.9$ and the dotted lines correspond to groups in which the signal-quality correlation $\rho = 0.5$. Parameters: unless the parameter is being varied $\delta = 0.5$, $\ell_i = 0.2$, $N = 50$, $p_o = 0$, $\sigma_b = 0.2$, $\sigma_i = 0.01$, $\sigma_q = 0.5$, $T = 10000$, $w = 1100$.

slightly decreases or stays constant (Figure 2B,C). Longer memory windows more effectively reduce error for animals using individual recognition. For animals using the badge system with moderate category widths, they encounter other animals in the same category so often that they rarely forget their opinions before the memory window has elapsed. Only when category width is very small does increasing memory window have a significant effect on error (SI?? Figure S6). When we compared learning for two badge signals, one with a high badge to quality correlation and one with lower badge to quality correlation, we find that badges with higher correlations with quality always outperformed badges with lower quality correlations (Figure 2, solid vs dashed red lines). Animals using the badge system learn more accurately and more quickly when the the signal and quality are more strongly correlated.

When the signal is highly correlated with quality, an intermediate category width minimizes error (Figure 2). This pattern can be explained as follows. Regardless of the signal-quality correlation, as category width increases, the number of animals in a given category increases (Figure S2). The first consequence of this is that an animal trying to learn about a single category will encounter it more often and be less likely to forget its opinion of it before its memory window lapses, assuming its memory window is finite. This tends to decrease the error with which animals can learn about their peers. The second consequence is that each time an animal encounters a category it extrapolates the information it gathers to more animals. This tends to increase learning error. When the badge is poorly correlated with quality, this increase in error due to increased confusion is much greater than the decrease in error due to a lower chance of forgetting so that as category width increases error increases as well. However, when the badge is highly correlated with quality, the increase in error due to increased confusion is much less pronounced because animals with similar badges do actually have similar quality values. Therefore, as category width increases, at first error decreases because of the reduced probability of forgetting and later it increases because of increased confusion. Similarly, an intermediate category width minimizes learning time when the badge-quality correlation is high. When the memory window is infinite, there is no decrease in error because there is no chance of forgetting what has been learned (Figure S6).

The effect of observational learning

Observational learning helps animals using both systems to learn more accurately and more quickly, but it helps animals using individual recognition much more (Figure 3). Observational learning increases the number of animals about which a focal animal can learn at any given time. Observational learning increases the number of animals about which a focal animal can learn at any given time; since animals using the badge system already learn about multiple animals at once, increasing the probability of observing interactions does not have a strong effect on learning rates in badge systems. In fact, for animals using individual recognition, the same level of error can be achieved by increasing the probability of observing (p_o), by increasing memory window (w), or by increasing both to a lesser degree. The same is true of learning time. This can be seen in the strong interaction in how error and learning time change as a function of the probability of observing (p_o) and memory window (w) (Figure 3).
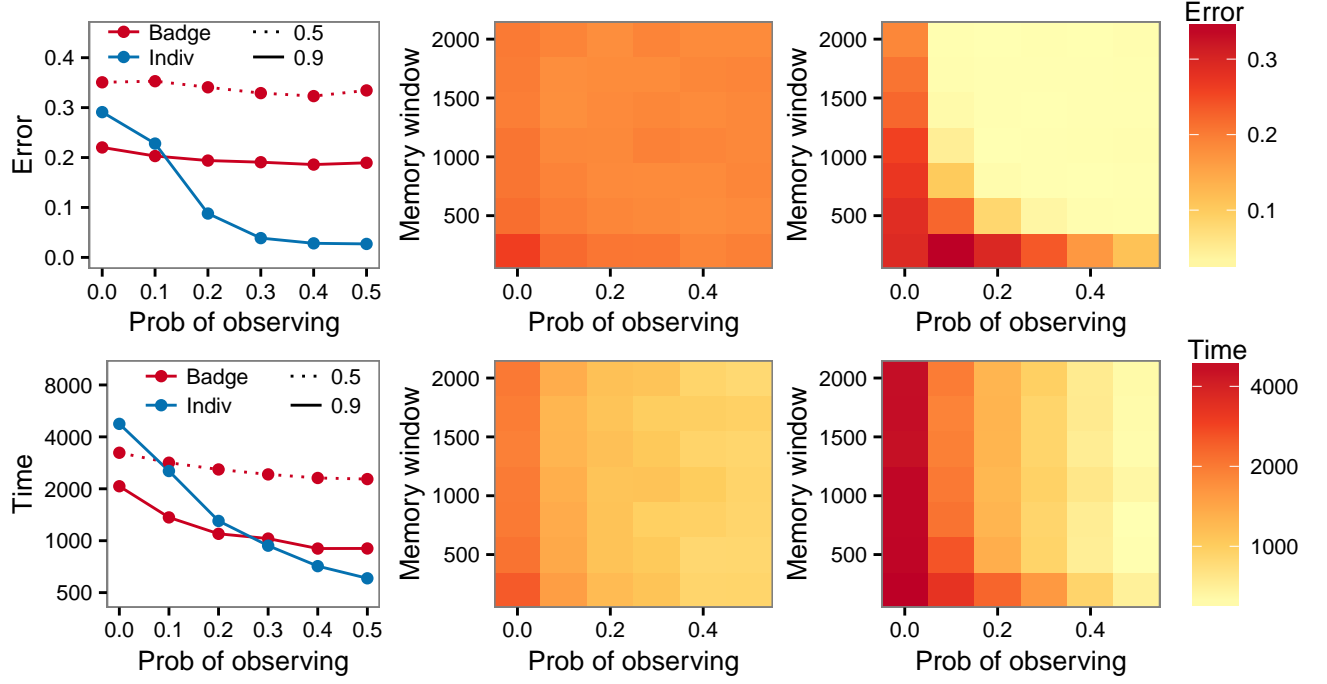
Figure 3: **Observational learning improves both error and learning time and does so much more for animals using individual recognition.** For animals using individual recognition, there is a strong interaction between the probability of observing and memory window. In A and D, we show average error $\bar{\epsilon}$ and average learning time $\bar{\tau}$ respectively as a function of the probability of observing, p_o. In each panel, blue lines show animals using individual recognition and red lines show animals using the badge system. The solid red lines correspond to groups in which the signal-quality correlation $\rho = 0.9$ and the dotted lines correspond to groups in which the signal-quality correlation $\rho = 0.5$. In B and C we show average error $\bar{\epsilon}$ of animals using the badge system and individual recognition respectively as a function of both the probability of observing p_o on the horizontal axis and memory window w on the vertical axis. In E and F we show average learning time $\bar{\tau}$ of animals using the badge system and individual recognition respectively as a function of both the probability of observing p_o on the horizontal axis and memory window w on the vertical axis. Parameters: in all panels $\delta = 0.5$, $\ell_i = 0.2$, $\ell_o = 0.2$, $N = 50$, $\sigma_b = 0.2$, $\sigma_i = 0.01$, $\sigma_o = 0.01$, $\sigma_q = 0.5$, $\rho = 0.9$, $T = 10000$; in A and D $w = 1100$, in B and E $\rho = 0.9$.

Cost of learning

Since increasing group size increases both error and learning time (Figure 2A,B), it also increases the overall cost of using both learning systems (Figure 4A). The effects of memory window (w) and category width (δ) on overall cost depend on the cost function, specifically on the parameter α (Figure 4B,C). When $\alpha < 1$, the costs of memory window (c_w) and category width (c_δ) increase most quickly at low cognitive ability; when $\alpha > 1$, the costs of memory window and category width increase most quickly at high cognitive ability (Figure S4).

When the costs of the memory window increase quickly at low w ($\alpha < 1$), the rapid increase in the cost of using a longer memory window is almost exactly offset by the decrease in error and learning time, so the costs of using both systems are almost a constant function of memory window (Figure 4B). However, when the cost of memory window increases quickly at high w ($\alpha > 1$), overall costs initially decrease as w increases because of the improvement in error and learning time and only eventually increase because of the cost of using a longer memory window, so an intermediate memory window is the least costly (Figure 4B).

Using a category width δ equal to 0 is always costly because it leads to high error and learning time, as we saw above (Figure 2E,F). When the costs of category width increase quickly as δ decreases from 2 ($\alpha < 1$), overall costs tend to increase as δ decreases, but there is a large range of intermediate δ at which overall costs are nearly constant: in this range, the increase in cost from decreasing δ is offset by a decrease in cost from reduced error and learning time. When the costs of category width increase only at low δ ($\alpha > 1$), at first decreasing δ decreases overall cost by improving error and learning time and only at low δ does overall cost increase because of the higher cost of this cognitive ability: an intermediate category width is favored (Figure 4C).

The overall costs of using the badge system are higher than the costs of using individual recognition when group size is small and memory window is long (Figure 5A,C). In these cases, animals using individual recognition are capable of learning accurately about their peers and there is no benefit from grouping animals together into categories. When the signal-quality correlation is high, individual recognition is only better for very small groups and very long memory windows (Figure 5C).

At an intermediate group size ($N = 50$), animals using individual recognition perform similarly to or better than animals using the badge system when category width is small and memory window is long (Figure 5B,D). In these cases, animals using the badge system are paying high costs for their cognitive abilities without receiving much benefit from either improved error or improved learning time. When the signal-quality correlation is high, individual recognition is more costly except when category width is equal to 0 and the two systems are equivalent (Figure 5D).

Discussion

Accurate assessment of the quality of conspecifics is important in many contexts, but the conditions under which different assessment systems may be favored is not well understood. Here, we modeled quality assessment in social groups, with animals using either a badge signal, which allows them to group others into quality categories based on the intensity of the badge, or individ-
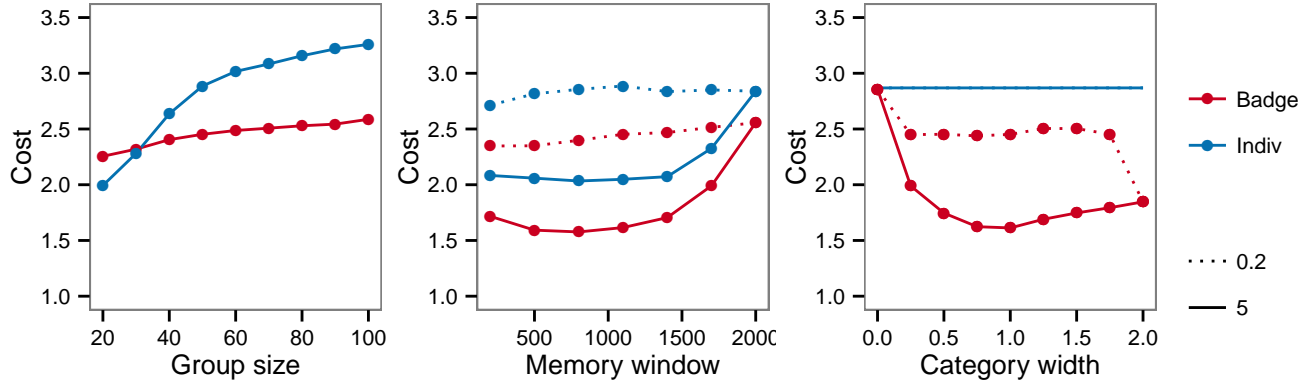
Figure 4: **Overall costs are lowest in small groups and with intermediate memory window and category width, when costs increases at high cognitive abilities ($\alpha > 1$).** When costs increase at low cognitive abilities ($\alpha < 1$), memory window w does not affect overall costs and large category width δ minimizes overall costs. In A,B, and C, we show overall costs C as a function of group size N, memory window w, and category width δ respectively. In each panel, blue lines show animals using individual recognition and red lines show animals using the badge system. The solid lines correspond to $\alpha = 5$ and the dotted lines correspond to $\alpha = 0.2$. Parameters: unless the parameter is being varied $\delta = 0.5$, $\ell_i = 0.2$, $N = 50$, $p_o = 0$, $\rho = 0.9$, $\sigma_b = 0.2$, $\sigma_i = 0.01$, $\sigma_q = 0.5$, $T = 10000$, $w = 1100$.

ual recognition, where they remember the outcomes of events involving each particular individual. Our goal was to better understand the costs and benefits of each system and the conditions under which each system might be favored.

Summary of results (no costs) and implications

In the absence of observational learning, smaller groups and longer memory duration make it easier to learn in both learning systems, which is consistent with general intuition. While the sign of the effect of increasing group size was the same in the two systems, the extent of the effect differed between. Assessment error and learning time were much more affected by increasing group size in the individual recognition system than the categorical badge system. We also find that agents using the badge system learn more quickly and accurately when there is a strong correlation between the signal and quality. While the correlation values we use are a bit higher than those estimated in species for which this data has been collected (XXX paper wasps [11], house sparrows [12], swamp sparrows [7], see Table S1 for details), our model shows that even with a moderate correlation the badge system is an effective way to learn about one's group mates.

We also find that animals using the badge system could minimize both the error with which they learned and their learning time by having a moderate ability to discriminate between different badges (i.e. by using an intermediate category width), as long as the badge was highly correlated with the underlying quality. This is somewhat counterintuitive as one might expect that it would always be advantageous to improve one's cognitive abilities. Our finding is related to the bias-variance tradeoff in statistics and machine learning: as a statistical model becomes more complex, it is more likely that its predictions will be accurate, but its predictions become more contingent on the training set and are therefore more variable XXX. Similarly, as animals increase the number of
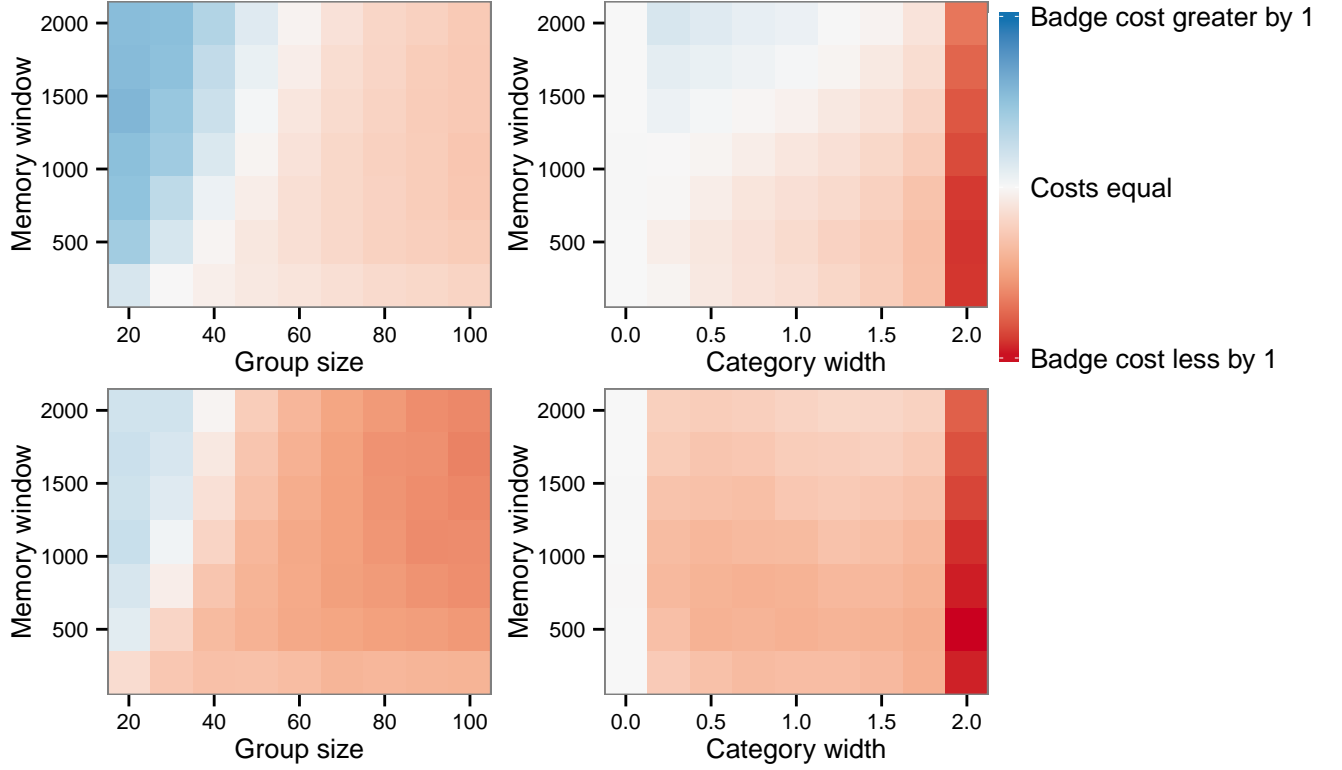
Figure 5: **The overall costs of using individual recognition are lower than the costs of using the badge system at low group size, high memory window, and low category width.** When the signal-quality correlation ρ increases, animals using the badge system incur lower costs for more combinations or parameters. Here we show the difference in the overall costs (C) associated with individual recognition and with the badge system as a function of A,C group size N and memory window w and B,D category width w and memory window w. Red indicates the badge system is less costly and blue indicates individual recognition is less costly. Parameters: in A and B $\rho = 0.5$, in C and D $\rho = 0.9$; unless the parameter is being varied $\delta = 0.5$, $\ell_i = 0.2$, $N = 50$, $p_o = 0$, $\sigma_b = 0.2$, $\sigma_i = 0.01$, $\sigma_q = 0.5$, $T = 10000$, $w = 1100$.

273 categories into which they place their peers, it becomes easier for them to learn accurately about
274 each of those categories, but they forget their assessments more quickly and therefore have more
275 variable assessments over time.

276 One explanation for why animals have imperfect cognition is that there are costs involved in im-
277 proving their cognition XXX [4]. However, our results suggest that imperfect cognition itself may be
278 adaptive. This may explain empirical examples of imperfect cognition (e.g. [6] XXX). Other studies
279 have also found that the most advanced cognitive strategies are not always optimal [2, 3, 5, 10].
280 Our work therefore contributes to our growing understanding of the circumstances that do or do
281 not lead to the evolution of sophisticated cognition.

282 When we allow the animals in our model to learn by observing interactions between other pairs
283 of animals, they are able to learn more quickly and accurately in both systems, but observational
284 learning was more beneficial for animals using individual recognition. While previous work has
285 shown the benefits of observational learning XXX, our study is the first to show that this depends
286 on how learning occurs int the first place. Our finding is somewhat surprising because one might
287 expect that making more observations helps animals using the badge system to make up for
288 the deficit inherent in their categorical method of learning. However, our finding agrees with /
289 Indeed, our finding disagrees with XXX Many animals that use individual recognition also use
290 observational learning XXX. Scientists have argued that this is because both individual recognition
291 and observational learning require advanced social cognition, of which animals using a badge
292 system are not capable XXX. However, our results suggest that it may be because it is precisely
293 in those species that observational learning is most advantageous.

Summary of cost results and implications

295 We find that, depending on how quickly the explicit costs of cognitive traits increase as the traits
296 improve, the costs of using either strategy are minimized by either not investing at all in cognition
297 or investing in a moderate cognitive trait (either memory window or perceptive ability). We find
298 no cases where the benefits of using the most advanced cognitive trait available (either a very
299 long memory window or category width equal to 0) outweighed the cost of using such a trait. This
300 finding reinforces previous studies that showed how difficult it is for advanced cognition to evolve
301 XXX [5].

Evolution of assessment systems

303 We find that the categorical badge system is usually less costly than individual recognition, except
304 when group sizes are small or their cognitive abilities are sophisticated. Not surprisingly, the
305 higher the correlation between the badge and quality, the greater the advantage of using the badge
306 system, since the badge becomes a more informative signal of the property animals are trying to
307 estimate. With a long memory window and a strong correlation between badge and quality, the
308 badge system was preferable in groups with more than about 30-40 individuals; with a weaker
309 correlation between badge and quality, groups had to be larger than about 50-60 individuals in
310 order for the badge system to be preferable. The advantage animals using the badge system
311 have over animals using individual recognition increases as their cognitive abilities diminish, since

312 their performance is not strongly affected and they pay fewer costs for investing in cognition. This
313 finding agrees with previous studies that found that individual recognition is most useful in small
314 groups XXX [12]. In particular, Dunbar has argued that early human societies were limited by the
315 number of other people a person can effectively learn about XXX. While our threshold of a group
316 size 50-60 is not identical to his threshold of a group size of 150, they are of the same order of
317 magnitude. Our finding also agrees with previous studies of badges of quality, which have found
318 that badges are more likely to evolve in large groups with poor cognitive ability XXX. By explicitly
319 comparing the two systems, we have generated a prediction about the types of groups and species
320 in which we expect one or the other system to evolve. Testing this prediction is left for future work.

Future steps and Conclusion

322 By studying a rather simple model, we were able to identify the conditions under which each
323 system is most effective and under which one or the other system should evolve. There are further
324 steps towards improving the realism of the model that will also improve our predictions about the
325 evolution of the two learning strategies. XXX

326 Our study shows that is not enough to study the conditions that could allow for the evolution of
327 a particular type of learning. By considering and comparing two solutions to the same biological
328 problem we find that different conditions favor different solutions.

15

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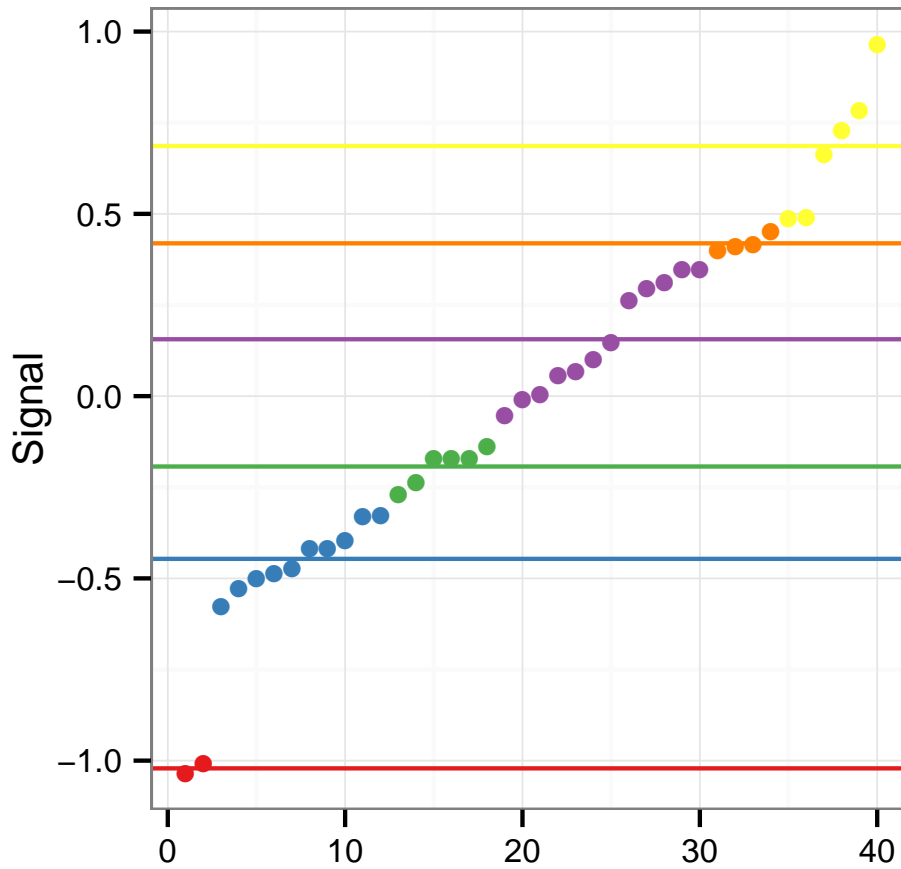
Supporting information

Figure S1: **Example of how categories are defined.** Here we show how a group of size $N = 40$ might be divided into categories with maximum width 0.5. Each point corresponds to an animal in the group. We show the signal of each animal on the y-axis and the order of the animals from lowest to highest signal on the x-axis. The color of the point indicates the category to which it belongs and the horizontal lines show the median signal value for each category. Categories were formed by choosing an animal i at random, putting all other animals whose signals were within $\delta/2$ of i's signal s_i into the same category, then choosing another uncategorized animal at random, and continuing until all animals were categorized.
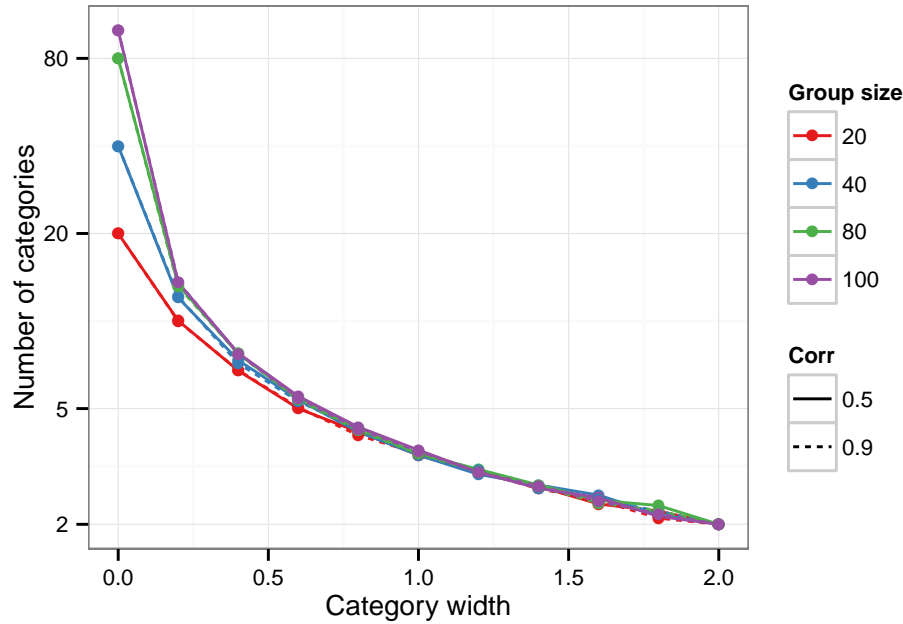
Figure S2: **As category width δ decreases the number of categories into which the group is divided increases.** For a given group size N and category width δ we generated a group with N signal values $\{s_i\}$ and categorized the group according to the procedure in the text and Figure S1 100 times and took the average number of categories across these 100 groups. Here we show how the average number of categories into which a group is divided depends on group size N and category width δ. Each colored line corresponds to a group size. There are overlapping solid and dotted lines in each color since the signal-quality correlation ρ does not affect the number of categories formed. When $\delta = 0$ there are as many categories as there are animals in the group. When $\delta = 2$ there are on average 2 categories, although it can happen that all animals are put into the same category.

Table S1: Examples of the correlation between a badge and a measure of fitness.

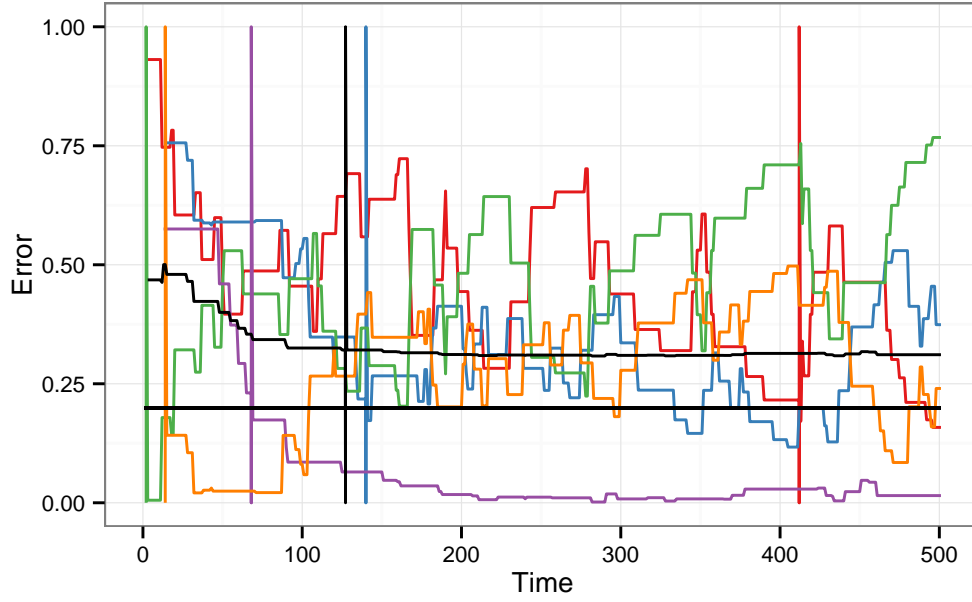| Species	Badge	Measure of fitness	Reference	
paper wasp	percent black on face	body size (head width)	$r^2 = 0.36$ for wasps with ≥ 2 black spots	[11]
	"badge brokenness"	dominance	$r^2 = .105$ (multivariate)	[11]
house sparrow	size of black bib	physical condition	$r = 0.379$	[12]
swamp sparrow	size of rusty cap	parental investment	$r^2 = 0.33$	[7]
	size of black forehead	aggression	$r^2 = 0.41$	[7]

Figure S3: **Example of how to calculate learning time.** Learning time τ_i can be less than T, even if average error at time T is above the threshold 0.2. Each colored line shows how one the error in one animal's opinion of its five group mates changes over time. The black line is its average error about the other animals, $\epsilon_i(t)$. The horizontal black line is the error threshold, 0.2. Each vertical colored line is the first time when corresponding line drops below the threshold. The vertical black line is the average of these learning times, τ_i.
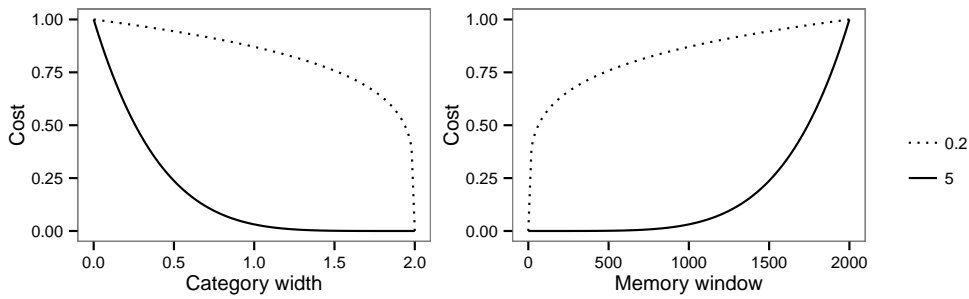
Figure S4: **Cost functions.** Here we show how the cost functions for the cognitive parameters category width and memory window. In each panel, the solid line corresponds to $\alpha = 5$ and the dotted line corresponds to $\alpha = 0.2$.
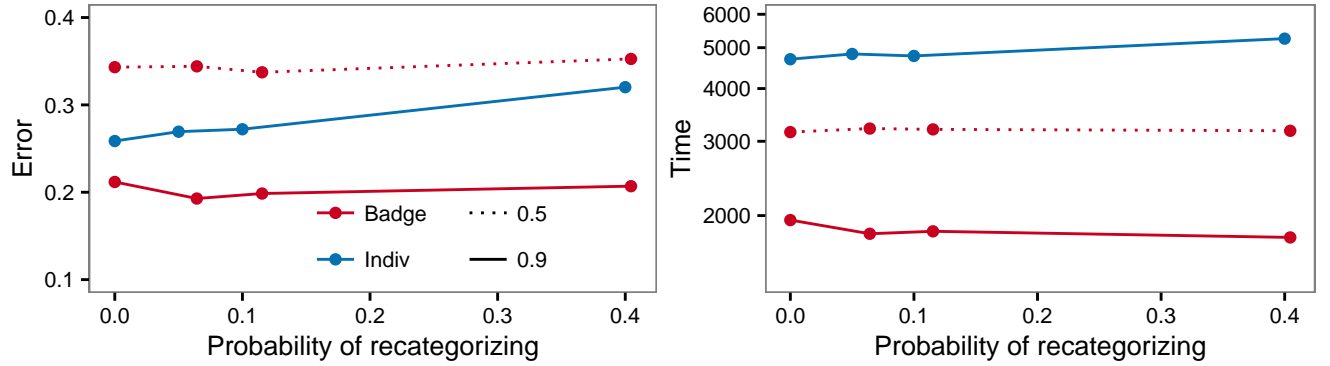
Figure S5: **Increasing the probability of being confused increases error and learning time in the individual recognition system and decreases error and learning time in the badge system.** Error and learning time are minimized at an intermediate category width. In the left pane, we show average error $\bar{\epsilon}$ as a function of the probability of recategorizing, and in the right panel, we show average learning time $\bar{\tau}$ as a function of the probability of recategorizing. In each panel, blue lines show animals using individual recognition and red lines show animals using the badge system. The solid red lines correspond to groups in which the signal-quality correlation $\rho = 0.9$ and the dotted lines correspond to groups in which the signal-quality correlation $\rho = 0.5$. Parameters: $\delta = 0.5$, $\ell_i = 0.2$, $N = 50$, $p_o = 0$, $\sigma_b = 0.2$, $\sigma_i = 0.01$, $\sigma_q = 0.5$, $T = 10000$, $w = 1100$.
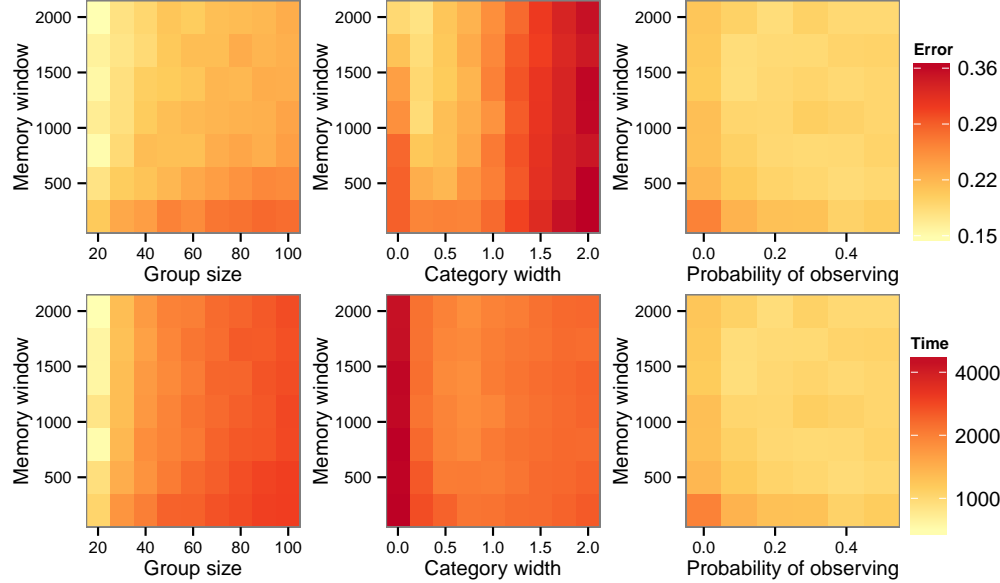

Figure S6: **Parameter interactions for animals using the badge system.** In A, B, and C we show average error $\bar{\epsilon}$ for animals using the badge system as a function of two parameters. In D, E, and F we show average learning time $\bar{\tau}$ as a function of two parameters. Parameters: unless the parameter is being varied $\delta = 0.5$, $\ell_i = 0.2$, $N = 50$, $p_o = 0$, $\rho = 0.9$, $\sigma_b = 0.2$, $\sigma_i = 0.01$, $\sigma_q = 0.5$, $T = 10000$, $w = 1100$.
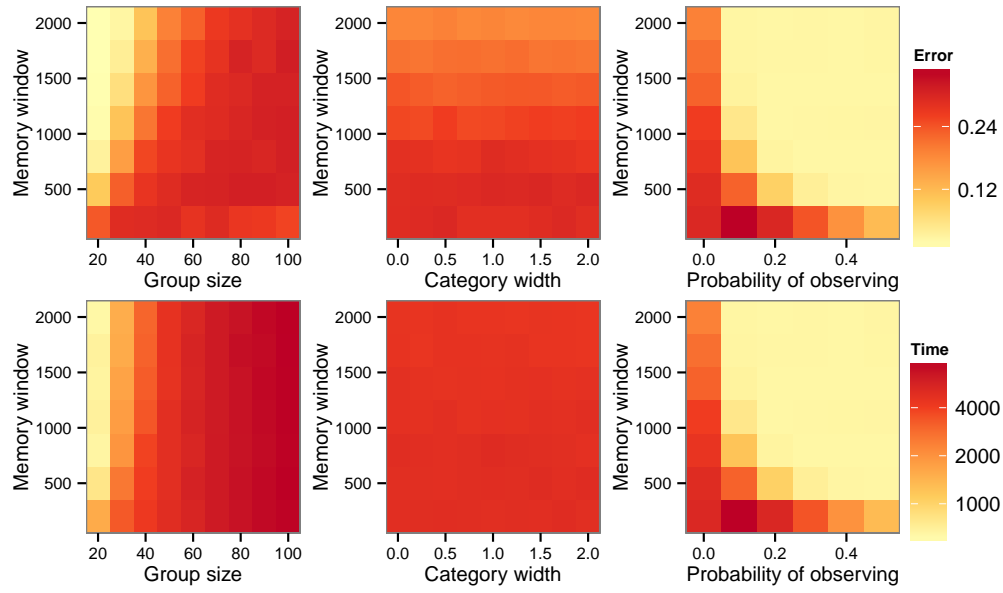
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Figure S7: **Parameter interactions for animals using individual recognition.** In A, B, and C we show average error $\bar{\epsilon}$ for animals using individual recognition as a function of two parameters. In D, E, and F we show average learning time $\bar{\tau}$ as a function of two parameters. Parameters: unless the parameter is being varied $\delta = 0.5$, $\ell_i = 0.2$, $N = 50$, $p_o = 0$, $\rho = 0.9$, $\sigma_b = 0.2$, $\sigma_i = 0.01$, $\sigma_q = 0.5$, $T = 10000$, $w = 1100$.