

Maths

January 12, 2012

1 Introduction

Pigtailed macaque society exhibits multi-scale structure spanning three organizational levels: a network of agonistic interactions, a network of subordination signaling interactions that emerges from the outcome of the agonistic interactions, and a distribution of social power that is encoded in the topology of the signaling network. Data suggest that individuals use information about their relative power to make decisions about which behavioral strategies to use in both agonistic and pro-social interactions. The data also suggest that individuals use information about their relative power, rather than fight outcomes, to inform strategic decisions because, as a coarse grained variable, power changes more slowly than fight outcomes (which can vary with context) and hence is a better predictor of interaction cost. In addition it appears that heavy-tailed power distributions can support novel forms of conflict management like policing. Little is known however about how different distributions of power arise.

Here we use data on the mechanistic causes of subordination signaling to build models exploring how factors influencing the decision to signal and number of signals accumulated, like the distribution of fighting abilities, error rate, and interaction rate, effect the type of power distribution that arises. We develop a series of null models to determine what kinds of power distributions arise from a relatively simple process like symmetry breaking, and whether such processes can recover our observed distribution. We then explore more complicated models.

2 Empirical Background

In previous work we studied how power is encoded in the signaling network. We tested the empirical and mathematical validity of alternative algorithms for computing power scores using directed subordination signaling network data collected from a group of captive, socially-housed pigtailed macaques housed at the Yerkes National Primate Research Center in Lawrenceville, Georgia. We operationalized social power as consensus among group members that an individual is capable of using force.

In the pigtailed macaque study system, the exchange of a subordination signal is an indication that the sender perceives the intended receiver as capable of using force. The signal is emitted after the sender has learned from a history of fights with its receiver, that it is likely to lose. Typically the perception by the sender of an agonistic asymmetry must be large for the exchange to take place. This means that the signal should be unidirectional.

In our study group there are 48 socially mature individuals. We label these 1, ..., 48, giving us a subordination signaling matrix S of size 48. We find that over the approximately four months of data collection, there were two pairs that signaled both ways: (3, 4) and (17, 24). 4 signaled to 3 three times and 3 to 4 once. The other pair signaled once each to each other. Despite these two pairs, signal exchange in this group is 99% directionally consistent over all pairs of individuals exchanging signals, which is consistent with expectation that the signal is unidirectional. The anomalous behaviour is potentially explained by signaling errors, since it is rare, or it could reflect a change in the direction of the pairs' dominance relationships that occurred at some point during the four months of observation.

The data suggest that the signal reduces receiver uncertainty about the state of the relationship and communicates agreement to a subordination contract, which holds as long as the sender perceives a asymmetry in the capacity to use force. We have proposed elsewhere that signal unidirectionality coupled to the fact that the subordination contracts change slowly compared to fight outcomes produces a subordination signaling network that can reliably encode how much consensus there is in the group about individual i 's capacity to use force.

Considering the graph where the individuals are nodes and the directed edge from a to b indicates that a has signaled at least once to b . It can be proven that if the graph is connected and transitive, then the individuals can be ordered according to the signals they receive, with signaling occurring up (and only up) the hierarchy. In much of the dominance hierarchy literature, if a statistically significant level of transitivity is observed, an algorithm is implemented that ranks individuals by minimizing inconsistencies along the diagonal.

Although this approach has its uses, it is not appropriate when the goal is to quantify consensus about the ability to use force successfully in the service of determining how particular distributions of power arise. This requires allowing for the possibility of other distributions beside the uniform distribution implied by an ordinal rank order. In addition, no assumptions should be made about transitivity as it is precisely because of the possibility of these relationships that we are interested in consensus. And, in fact, in our data set X relationships are intransitive. Furthermore we observe that there are 426 pairs with no signal exchange. A pair has probability 0.622 to have had at least one signal.

To quantify consensus about an individual's capacity to use force, we tested several diffusion-based and information theoretic algorithms by asking which a) had mathematical properties desired in a consensus formalism and b) produced a distribution of power that best predicted independent data that should be predicted by any good power measure.

We found that the number of signals received by individual i multiplied by the entropy of individual i 's signal received distribution best captures consensus about the ability to use force successfully. We refer to power computed this way as *Shannon Power*.

In our study group, the distribution of Shannon Power is not significantly different than log-normal and is shown in Figure X. Here we use two simple variants of this formalism—the number of signalers and the number of signalers multiplied by the total frequency of signals received—to study the dynamics by which a power structure arises. We show the distribution of both variants as observed in our data in Figure X. Figure X also shows that signals received increases with interaction rate, where interaction frequency is defined as [jess: give definition].

3 Model

We now explore the behavioral dynamics underlying different distributions of power. [Simple model explanation to go here]

In the current simple version of the model, the opinion matrix is always antisymmetric.

3.1 $\epsilon = 0$



When submission signaling is error-free, any pair of monkeys will fight only once. Following a fight in which individual i beats individual j , M_{ij} becomes -1 and M_{ji} becomes 1 and, forever after, j gives i a submission signal, thus averting fights. If the simulation runs for long enough, all pairs will have encountered each other and so M will be an antisymmetric matrix with 1 s and -1 s off the diagonal.



In this case, the number of individuals signaling to monkey i will be $\frac{\sum_j M_{ji} + (n-1)}{2}$, which is distributed between 0 and $(n-1)$ (and whose sum across individuals is $\frac{n(n-1)}{2}$).

3.2 $\alpha = 0$

In the case of no differences in fighting ability, the outcome of each fight is equivalent to the outcome of a fair coin toss, so the number of individuals that individual i beats in a fight is binomially distributed with distribution $B(n-1, 1/2)$. Under this scenario an individual's number of signalers will be distributed as $B(n-1, 1/2)$. This is well-approximated by the normal distribution $N((n-1)/2, (n-1)/4)$ ¹, for realistic values of n .

For comparison with the results of numerical simulations [KAREN: at this point, we have no numerical simulations so we need to change the wording here to make clear we are comparing to the observed data], we show in Figure S1 the probability density functions corresponding to $B(49, 1/2)$ and $N(24.5, 12.25)$. These compare with figure 8(d), where we note that that figure is a histogram, with bin size one and shows the number of primates

¹the second parameter is the variance not the standard deviation

out of 50 in each bin, so that to compare with the probability density function, we would need to divide the numbers by 50. We see that the results of a single simulation, whilst leading to a peaked distribution, deviate significantly from the probability density function. In order to obtain this distribution, we would need to average over multiple simulations. However it is extremely unlikely that the distribution would approximate the distribution of signaler number observed in the data (Figure X). [KAREN: still need to show that this also does not recover signaler number multiplied by total frequency, correct?]

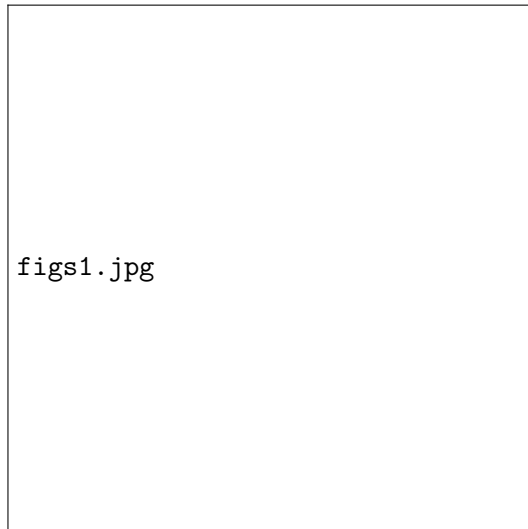


Figure 1: Plots of the probability density functions of $B(49, 1/2)$ (blue) and $N(24.5, 12.25)$ (red)

Signals only start to be accrued after the first encounter. Consistent with the data indicating signal unidirectionality, the signals are always in one direction within each pair. For an individual i who receives signals from $N(i)$ other individuals, the number of signals received, $S(i)$, will be Poisson distributed,

$$S(i) \sim \text{Poisson}(\lambda N(i)t), \quad (1)$$

where λ is the rate at which one pair of individuals interacts and t is time.

Signaling does not affect the establishment of the $N(i)$. Therefore ignoring the few signals which occur before all $N(i)$ are established,

$$\Pr(S(i) = k) \approx \sum_{l=0}^{n-1} \Pr(N(i) = l) \Pr(S(i) = k | N(i) = l)$$

$$\begin{aligned} P(N(i)=l) & \leftarrow \left(\frac{1}{2} \right)^{n-1} \sum_{l=0}^{n-1} \binom{n-1}{l} \frac{(\lambda l t)^k}{k!} e^{-\lambda l t} \quad \text{Poisson} \\ & \sim \text{Binomial} \\ & = \left(\frac{1}{2} \right)^{n-1} \frac{(\lambda t)^k}{k!} \sum_{l=0}^{n-1} \binom{n-1}{l} l^k e^{-\lambda l t}. \end{aligned} \quad (2)$$

[[Jesse- I haven't found a nice simplification of this, however it is possible to plot the distribution, if needed.]]

These results suggest that a simple symmetry breaking process, with no initial differences in fighting ability, gives rise to a roughly normal distribution of signaler number and hence cannot recover the distribution of signaler number observed in the data.

3.3 $\alpha \neq 0, \epsilon = 0$

In the case of differences in fighting abilities, the outcome of a fight is equivalent to a weighted coin toss. Let $p_{ij} = \frac{e^{\alpha(f(i)-f(j))}}{1+e^{\alpha(f(i)-f(j))}}$ be the probability that an individual i beats individual j . The number of individuals signaling to individual i will then be

$$N(i) = \sum_{j=1, j \neq i}^n X_{ij},$$

where X_{ij} are independent Bernoulli random variables with $X_{ij} \sim \text{Bernoulli}(p_{ij})$.

$N(i)$ has Poisson binomial distribution with parameters $p_{i1}, \dots, p_{ii-1}, p_{ii+1}, \dots, p_{in}$. Note that $E(N(i)) = \sum_{j=1, j \neq i}^n p_{ij}$ and $\text{Var}(N(i)) = \sum_{j=1, j \neq i}^n p_{ij}(1 - p_{ij})$. As before $\sum_i N(i) = \frac{n}{2}(n-1)$ and $N(i)$ is distributed between 0 and $n-1$.

When α is small $p_{ij} \approx \frac{1}{2}[1 + \alpha(f(i) - f(j))]$ and the distribution will be close to $B(n-1, 1/2)$. The expectation of $N(i)$ is approximately given by

$$E(N(i)) = \frac{(n-1)}{2} + \frac{n}{2}\alpha(f(i) - \bar{f}).$$

If α is large, $p_{ij} \approx 1 - e^{-\alpha(f(i)-f(j))} \approx 1$, if $f(i) > f(j)$. Therefore the distribution of $N(i)$ will be uniform between 0 and $n-1$ with high probability if α is sufficiently large.

3.4 $\epsilon \neq 0$

When there are errors in subordination signals, then each pair of individuals will continue to interact ad infinitum (in probability).

prob i beats j

3.4.1 $\alpha \neq 0$

The opinion j has of i will perform a biased random walk with success probability p_{ij} . After N encounters, the opinion that j has of i is Z , where $Z = 2X - N$ and $X \sim \mathcal{B}(N, p_{ij})$.

When N is very large, this is well-approximated by

$$X \sim N(Np_{ij}, Np_{ij}(1 - p_{ij})),$$

provided α is not too large.

So

$$Z \sim N(N(2p_{ij} - 1), 4Np_{ij}(1 - p_{ij})).$$

Therefore, the probability that j will signal to i

$$\begin{aligned} &= 1 - \Phi_{Normal} \left(\frac{1 - N(2p_{ij} - 1)}{2\sqrt{Np_{ij}(1 - p_{ij})}} \right) \\ &= \Phi_{Normal} \left(\frac{N(2p_{ij} - 1) - 1}{2\sqrt{Np_{ij}(1 - p_{ij})}} \right). \end{aligned}$$

high Z
⇒ j is likely to signal

Without loss of generality, we assume that $p_{ij} > 1/2$, then the probability that j will signal to i

$$\approx 1 - Q \left(\frac{\sqrt{N}(2p_{ij} - 1)}{2\sqrt{p_{ij}(1 - p_{ij})}} \right).$$

Now for $x > 0$, $\frac{1}{\sqrt{2\pi}}e^{-x^2/2}\frac{x}{1+x^2} < Q(x) < \frac{1}{\sqrt{2\pi}}e^{-x^2/2}\frac{1}{x}$. So, assuming $\frac{N(2p_{ij}-1)^2}{4p_{ij}(1-p_{ij})} \gg 1$,

the probability that j signals to i is approximately $1 - \frac{\sqrt{2p_{ij}(1-p_{ij})}}{\sqrt{\pi N}(2p_{ij}-1)} e^{-\frac{N(2p_{ij}-1)^2}{8p_{ij}(1-p_{ij})}}$.

As $N \rightarrow \infty$, if $p_{ij} > 1/2$, the probability that j signals to i will tend to 1.

Thus, in the very long term (in probability), j will signal to i if and only if $f(i) > f(j)$.

Therefore, the signaler number distribution will be uniform.

Although rare mistakes may modify the distribution slightly, the number of signals received should hence roughly satisfy

$$\begin{aligned} \Pr(S(i) = k) &= \frac{1}{n} \sum_{l=0}^{n-1} \Pr(S(i) = k \mid N(i) = l) \\ &= \frac{1}{n} \sum_{l=0}^{n-1} \frac{(\lambda l)^k}{k!} e^{-\lambda l} \\ &= \frac{1}{n} \frac{(\lambda)^k}{k!} \sum_{l=0}^{n-1} l^k e^{-\lambda l}. \end{aligned} \tag{3}$$

This looks roughly uniform over a range of values from k not much greater than zero to k around $(n-1)\lambda t$. Again, we do not recover the observed distribution of signaler number. [KAREN: still need to show that this also does not recover signaler number multiplied by total frequency, correct?]

[[Jess- I do not have a proof yet that this look roughly uniform. I can plot it if necessary.]]

3.4.2 $\epsilon \neq 0, \alpha = 0$

In this case, again, given infinite time, i and j will encounter each other infinitely often (in probability). The opinion i has of j , M_{ij} undergoes an unbiased random walk. As $t \rightarrow \infty$, for each integer k , $\Pr(M_{ij} = k) \rightarrow 0$ and, in particular, $\Pr(M_{ij} = 0) \rightarrow 0$. By symmetry, $\Pr(M_{ij} > 0) = \Pr(M_{ij} < 0)$. Therefore as $t \rightarrow \infty$, $\Pr(M_{ij} \geq 1) \rightarrow 1/2$. So for each pair (i, j) , at late times, the probability that i signals to j tends to $1/2$.

Therefore (as for the case $\epsilon = 0$), the number of signalers to i is roughly distributed as $B(n-1, 1/2)$. In this case, in contrast to the case when $\epsilon = 0$, $N(i)$ is not fixed. Indeed, for any pair of individuals, the direction of the subordination signal should change infinitely many times as $t \rightarrow \infty$. This stands in contrast to the data, which indicate the directional consistency is nearly perfect over the data collection period. These results indicate that

3.5 Imperfect learning

Earlier in our analyses we assumed no differences in fighting ability as a simplification. However heterogeneity in fighting ability, due to differences in body size, experience, and size of alliance network, is well-documented. Here we explore the effect of $\alpha \neq 0$. We allow for the possibility that the monkeys occasionally fail to signal even when they perceive their opponent to be stronger, so that $\epsilon \neq 0$. Therefore, in the very long term learning limit, in our null model, we expect the number of signalers to a given individual to become uniformly distributed. Figure X shows the actual distribution of signalers to in a our study group.

The distribution in Figure X is not uniform and so we conclude that learning must be imperfect. Perfect learning would imply that signals are always given to stronger individuals. This will not be the case under error or when the asymmetry must be large in order for individuals to benefit from agreeing to be subordinate.

We modify the model in two ways to explore the impact of imperfect learning. The first way is to require that the opinion held by individual 1 of individual 2 must exceed a threshold higher than 1, in order for individual 1 to signal to individual 2. We are assuming that individuals must perceive a large asymmetry in order to emit a signal.

This assumption alone is likely to have little effect on the signaling matrix in the limit as learning time tends to infinity. The reason for this is that the net number of fights won by a stronger fighter against a weaker fighter should tend to infinity as time tends to

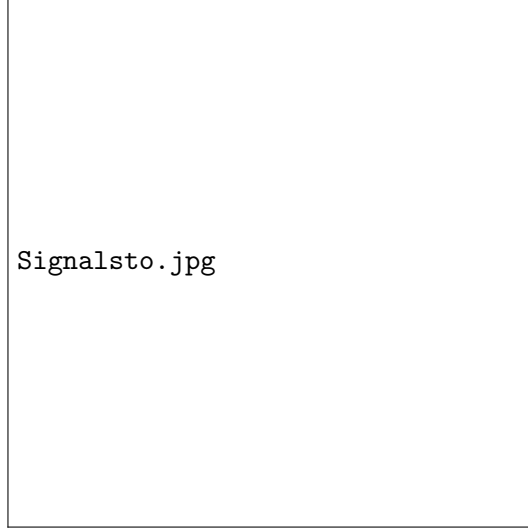


Figure 2: Experimentally derived distribution of number of signallers to in a population of 48 primates.

infinity because fight outcomes are governed by a biased random walk. This means that in the long time limit, the threshold required to emit a signal is largely irrelevant.

In practice, however, any pair of individuals will only have finite numbers of interactions on which to base their signaling decisions. In addition, their memory of the history of fight outcomes is likely to be limited. To capture the effects of finite sample size and memory constraints, we introduce a parameter that controls the rate at which individuals forget opinions (i.e. summed stored fight outcomes) over time. We assume that the opinion M_{ij} of one individual about another degrades. It is possible to keep this opinion as an integer and allow each unit to disappear stochastically with some rate. This is likely a more realistic way of modeling the forgetting of past encounters, as it allows stochasticity in the forgetting process. However, for computational simplicity, we assume a continuous degradation of the opinion, whereby the values M_{ij} are no longer restricted to be integral. If the degradation rate of the opinion is δ , then, roughly speaking, individuals make decisions based on fights occurring in a time interval $1/\delta$.

The expected value of the opinion individual i has of individual j will hence satisfy

$$\dot{\bar{M}}_{ij} = \lambda(1 - 2p_{ij}) - \delta\bar{M}_{ij}. \quad (4)$$

Thus at steady state,

$$\bar{M}_{ij} = \frac{\lambda(1 - 2p_{ij})}{\delta}. \quad (5)$$

Whether an individual signals to another will depend on the recent history of fight outcomes

and hence be stochastic, however, roughly we expect individual i to signal to individual j if

$$\frac{\lambda(1 - 2p_{ij})}{\delta} > \theta, \quad (6)$$

where θ is the threshold opinion that must held in order to signal. In reality, θ may also be distributed. Approximately, however, we expect signaling to occur when equation (??) holds. For any signaling to occur, we require $\theta < \frac{\lambda}{\delta}$. In this case, an individual i will signal to individual j roughly when $p_{ij} < \frac{1}{2} \left(1 - \frac{\delta\theta}{\lambda}\right) < \frac{1}{2}$.

We see that the threshold probability for i to beat j below which i will signal to j depends only on the ratio of λ and δ . However, the larger the values of these two parameters, the more deterministic the learning process is.

We specified that the probability for i to beat j was a monotonically increasing function of the differences in strength between i and j . Therefore if i signals to j when its probability to win in a fight against j is below a threshold (less than $1/2$), then this will happen if $(f(j) - f(i))$ is greater than a threshold value $\left(\frac{1}{\alpha} \ln \left(\frac{\lambda + \delta\theta}{\lambda - \delta\theta}\right)\right)$. We call this threshold t .

The signaler number distribution will hence depend on the underlying distribution of fighting abilities. We compute the distribution for a uniform distribution and for a normal distribution of fighting abilities and compare with Figure X.

For a uniform distribution of fighting abilities, $f \sim U[0, 1]$, we find that, for $k = 1, 2, \dots, n-1$,

$$\Pr(N(i) = k) = \binom{n-1}{k} \int_t^1 (x-t)^k (1-x+t)^{n-1-k} dx \quad (7)$$

$$= \binom{n-1}{k} \sum_{r=0}^k \frac{(-1)^r}{n-k+r} \binom{k}{r} \left[1 - t^{n-k+r}\right], \quad (8)$$

and

$$\Pr(N(i) = 0) = t + \frac{1 - t^n}{n}. \quad (9)$$

This reduces to the discrete uniform distribution for $t = 0$. When $t = 1/2$, we plot the distribution for $n = 50$:

Note it is straightforward to prove from (7) that $\Pr(N(i) = k) \leq 1/n$ for $k = 1, \dots, n-1$. Therefore, aside from the probability of having no signallers to an individual, being much elevated, the rest of the distribution cannot be too far from uniform. We see from the figure, in fact that the distribution is roughly uniform (close to $1/n$) until a little below $k \leq (1-t)n$ after which the probability mass function decays towards zero. The same is true, when $t = 0.1$, see figure 4.

For a normal distribution of fighting abilities, $f \sim N(0, \sigma^2)$, where we choose $\sigma = 1/(2\sqrt{3})$ to have the same variance as a random variate with distribution $U[0, 1]$, we find

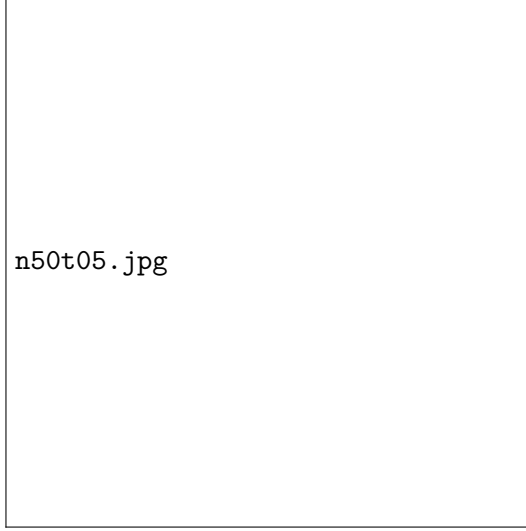


Figure 3: Distribution of signaler number when $n=50$, fighting ability is independently distributed as $U[0, 1]$ and the threshold difference in fighting abilities which is sufficient to engender signalling is $t = 0.5$.

that, for $k = 0, 2, \dots, n - 1$,

$$\Pr(N(i) = k) = \binom{n-1}{k} \int_{-\infty}^{\infty} f(x) F(x-t)^k (1-F(x-t))^{n-1-k} dx, \quad (10)$$

where $f(x)$ is the pdf of $N(0, \sigma^2)$ and $F(x)$ is its cdf.

When $t = 1/2$, we plot the distribution for $n = 50$:

When $t = 0.1$, we also plot the distribution for $n = 50$:

Finally, to show that it is possible to obtain a distribution similar to the one in Figure 2, we show the same plot with $t = 0.25$.

Then multiply the pdf by the number of individuals in the population to give a frequency distribution to compare with Figure 2 and we also put the data into bins 0 – 4 signalers to, 5 – 9, ..., 45 – 49. The distribution is given in figure 6.

[KAREN: as above still need results for signaler number multiplied by frequency received?] It looks like from the plots that we can roughly recover the distribution of signaler number for $t=0.1$. However as we discussed I think we will need to consider heterogeneity in interaction rate to recover the long tail that characterizes the signaler number multiplied by frequency distribution. This is one reason why I think we should include study of that distribution as well throughout the analyses.]

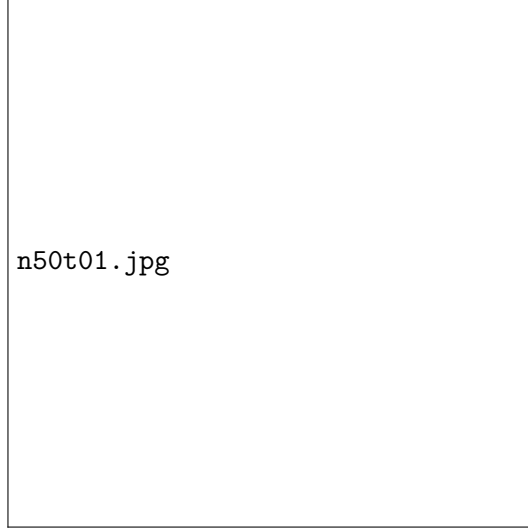


Figure 4: Distribution of signaler number when $n=50$, fighting ability is independently distributed as $U[0, 1]$ and the threshold difference in fighting abilities which is sufficient to engender signalling is $t = 0.1$.

3.6 Non-uniform interaction rate

Thus far we have not been able to recover the observed distribution of signaler number multiplied by frequency received. We observe that some individuals signal multiple times to a particular receiver. Although some variance in signals emitted is expected due to Poisson process of encounters, we doubt this can fully account for the data and explore below the consequences of introducing heterogenous interaction rate.

[Note: We have no model of the multiplicity of signaling at a single encounter. KAREN: multiple signals are not typically given during a single encounter. Signals are repeated over time. Conditional on i signaling to j , the number of signals i gives j should be identically Poisson distributed with the same mean and variance. SHOW THEY ARE NOT.]

We show the probability distribution of the number of signals one individual gives another provided this number is not zero in figure 7.

As shown in Figure X [Jess moved (at least in text) all empirical figures to data section at beginning of paper] plot the number of signals received against the number of signalers to and add a best-fit line. See figure 8. Clearly there is no straight line which fits the data well. Therefore it is not the case, that the signals received are proportional to the number of signalers to. We therefore now explore the case where the pairwise interaction rate is not constant across all pairs.

Previous work suggests that as the frequency of signals received by individual i in-

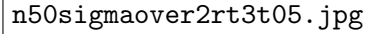


Figure 5: Distribution of signaller number when $n=50$, fighting ability is independently distributed as $N(0, 1/12)$ and the threshold difference in fighting abilities which is sufficient to engender signaling is $t = 0.5$.

creases, the cost of i 's social interaction decreases, and, consequently, i 's interaction rate increases. In further support of this conclusion, we observe (see figure1d- jess) that when total interactions are plotted against signals received, there is an approximately linear relationship, with gradient greater than one.

Considering the analysis of section 2.3, especially equation (4), we see that what happens depends on whether the individuals in the study system can remember a maximal number of past encounters or whether they can remember encounter for a maximal time. Increasing the interaction frequency with the number of signals received will alter λ .

In the case where the individuals remember a maximal number of encounters, δ also changes in proportion to λ and the steady state, as given in equation (6) is unchanged. Then roughly the number of signals received will be proportional to $\lambda \times$ the number of signallers to, where λ is an increasing function of the number of signallers to (the function appears to be close to linear, according to the data).

NO- NEED TO CONSIDER PAIRWISE INTERACTION RATE AS THE PRODUCT OF TWO PARAMETERS-[KAREN: what is this statement referring to?]

In the case where the primates remember interactions over a maximal timespan, the steady state opinions will be proportional to λ

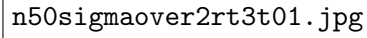


Figure 6: Distribution of signaller number when $n=50$, fighting ability is independently distributed as $N(0, 1/12)$ and the threshold difference in fighting abilities which is sufficient to engender signaling is $t = 0.1$.

4 Additional Questions

What could explain degree of observed transitivity? A small degree of intransitivity could be explained by signalling errors.

Are some primates unreliable signalers? I.e. are they inconsistent in whom they signal to? We can define a measure of the intransitivity of individual signallers.



Figure 7: Distribution of signaler number when $n=50$, fighting ability is independently distributed as $N(0, 1/12)$ and the threshold difference in fighting abilities which is sufficient to catalyze signaling is $t = 0.25$.

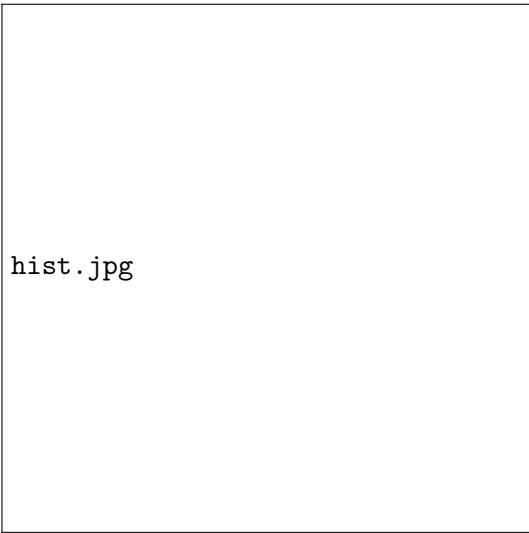


Figure 8: Binned frequency of signaler number to an individual when $n=50$, fighting ability is independently distributed as $N(0, 1/12)$ and the threshold difference in fighting abilities which is sufficient to engender signaling is $t = 0.25$.



Figure 9: Scaled experimental probability distribution of the number of signals one individual gives another given that this number is nonzero.



Figure 10: Scatter plot of the number of signals received against the number of signallers to.