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Reciprocal mutualism not altruism: immediate but not delayed time matching in chimpanzee social grooming

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Summary

• Reciprocity is often seen as an underlying mechanism of ongoing dyadic social relationships.

• The default assumption is that both parties are benefiting through a roughly equal investment in each other.

• Biological markets are where partner choice plays a role in maximizing benefits: you choose to interact with a partner likely to reciprocate.

• Allogrooming (social grooming) occurs when one individual cleans the fur and skin of another individual, which is valuable to the receiver hygienically and hedonically.

• Figure 1 is a depiction of allogrooming occurring amongst three individuals (A, B, C).

• Among chimpanzees and other primates, an ubiquitous currency of exchange are units of allogrooming (aka social grooming): the units being parcels of time invested when chimpanzee A grooms chimpanzee B (which carries assumptions of cost and benefits).
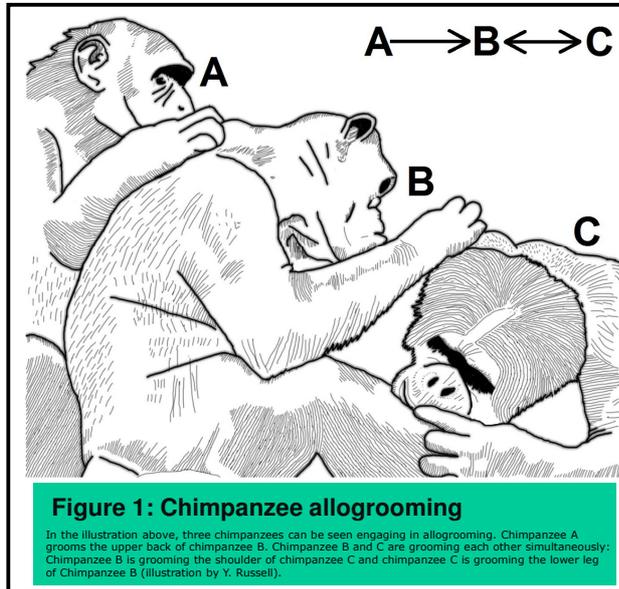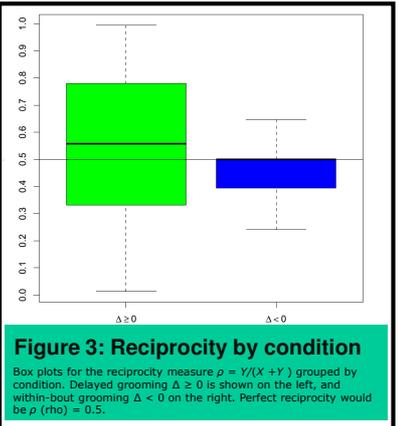
• Here, we examined tit-for-tat reciprocation of allogrooming in a group of 25 captive chimpanzees at Chester Zoo UK, focusing on three issues:

  1) Grooming relationships amongst all 325 possible dyads.

  2) Equally of effort within these dyads (i.e. time matching).

  3) Time horizons (time scales whereupon matching may occur)

• Time horizons were of particular interest (because immediate and delayed reciprocity are different:

  • Payback after a delay (such as in *reciprocal altruism*) entails periods of unseen reward and requires some mechanism (cognitive or otherwise) to bind together both parts of the transaction.

  • In contrast, payback without delay (*reciprocal mutualism*) requires merely a pay-as-you-receive heuristic.

• Using a generalised linear mixed-method, we found evidence for immediate reciprocation (within-bout grooming) but not for delayed reciprocation.

• Our analysis implies that previous claims of long-term grooming reciprocation amongst chimpanzees are possibly mistaken and that the real mechanisms involving grooming tit-for-tat involve partner choice and immediate reward.

Methods

• Twenty-five captive chimpanzees were observed at Chester Zoo, UK, in 2003-4 by Y. Russell.

• Mean age of the chimpanzees were 18.7 years (SD = 11.2), comprising five adult males, fifteen adult females, four subadult females, and two juveniles.

• We analysed a period of 44.25 hours (over 17 days).

• The investigator scanned groups continuously and recorded all individuals engaged in grooming cliques (identity of groomers, direction of grooming).

• Fig. 2 shows the model for analysis. Here, we used the word 'bout' to mean a grooming event with no interruption. Within-bout (immediate) reciprocation is thus where payback of grooming occurs while the other is still grooming you.

• An occurrence reliability score was calculated in an earlier publication: 84.86%.
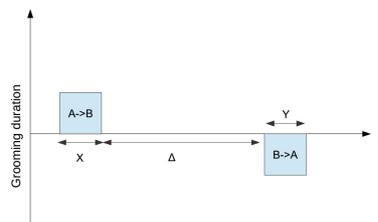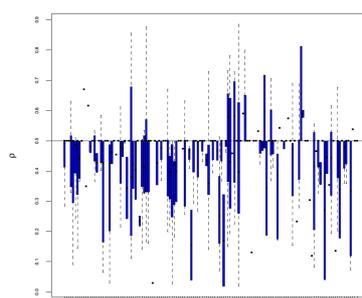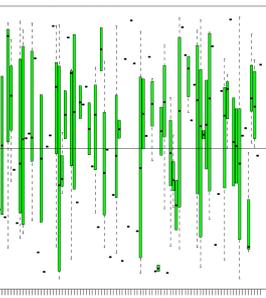

Figure 1: Chimpanzee allogrooming

In the illustration above, three chimpanzees can be seen engaging in allogrooming. Chimpanzee A grooms the upper back of chimpanzee B. Chimpanzee B and C are grooming each other simultaneously: Chimpanzee B is grooming the shoulder of chimpanzee C and chimpanzee C is grooming the lower leg of Chimpanzee B (illustration by Y. Russell).

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Figure 3: Reciprocity by condition

Box plots for the reciprocity measure $\rho = Y/(X + Y)$ grouped by condition. Delayed grooming $\Delta \geq 0$ is shown on the left, and within-bout grooming $\Delta < 0$ on the right. Perfect reciprocity would be ρ (rho) = 0.5.

Figure 2: Model for analysis

The model used for the longitudinal regression analysis. Consecutive or simultaneous pairs of grooming events between any given dyad $\{A, B\}$ are represented in our data-set by triples (X, Y, Δ), where: X represents the time that A spent allogrooming B; Y represents the time that B spent allogrooming A and Δ represents the time that elapsed between (i) A finishing grooming B, and (ii) B starting to groom A. Within-bout grooming is recorded using negative values of Δ.

(a) Null model

(b) Entire dataset

(c) Within-bout time-matching $\Delta < 0$

(d) Delayed time-matching $\Delta \geq 0$

Figure 5: Windowed time matching

Grooming durations summed over windows of 20m, 40m, 1h, 4h (see legend top left of each). Each figure represents (a) the null model, (b) durations of both immediate and delayed, (c) time-matching within bout, (d) time-matching after a delay.

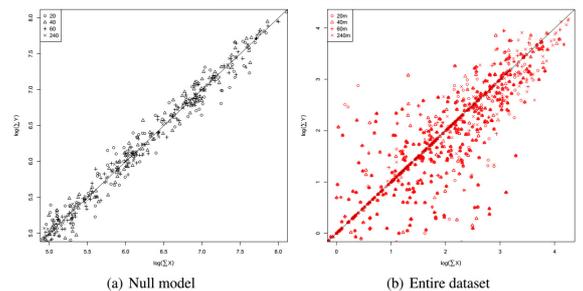(a) Reciprocity by dyad - $\Delta < 0$

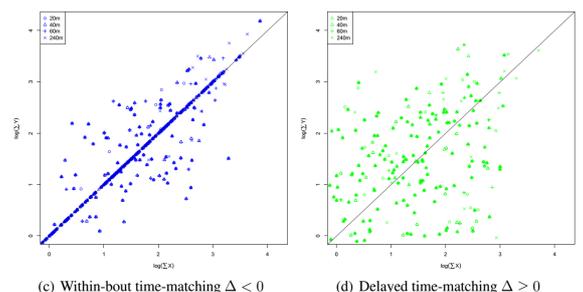(b) Reciprocity by dyad - $\Delta \geq 0$

Figure 4: Reciprocity by dyad

Box plots for the reciprocity measure $\rho = Y/(X + Y)$ grouped by condition: (a) immediate time-matching, $\Delta < 0$ is shown at the top and (b) delayed $\Delta \geq 0$ shown at the bottom. Perfect time-matching would be ρ (rho) = 0.5.

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Results

• Grooming occurred only in 45% of all possible dyads (146/325).

• Fig. 3 shows how time-matching compares in conditions of immediate ($\Delta < 0$) vs. delayed ($\Delta \geq 0$) situations. As shown, time matching more accurate in former.

• Fig. 4 shows the same for each dyad. As shown, there is great variability at the dyad level.

• Fig. 5 shows time-matching compared against a null model. As shown, there is time-matching that occurs in the null model. As shown, when we split the analysis into immediate and delayed time matching, the time-matching fidelity disappears in the delayed situation.

• We also performed a time-matching regression using a mixed-effects model using the dyad as a random effect in the intercept (not visualised here). We calculated mixed model estimates (standard errors). P-values were calculated using a likelihood ratio test with a null model comprising only the random effects. For within-bout time-matching, α = 68.43 (15.59), β = 0.66 (0.03), $p < .001$. For delayed time-matching, α = 246.10 (25.38), β = 0.049 (0.08), $p = .470$.

• We are not claiming that delayed reciprocation does not exist – but we have largely failed to find it here.

• We favour the explanation of *reciprocal mutualism*, whereupon, from a proximate point of view at least, time matching is more here-and-now. Functional effects across the lifespan are possible but not measured here.