

The origin of prosociality and fairness: Perspectives from experiments with orangutans

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Prosocial behavior, behaviors that produce benefits to others, has long been considered to be favored by natural selection, if it propagates the helper's genes via increased survival and reproduction of kin, or if it brings future benefits to the helper through direct or indirect reciprocation. The latter case, prosociality toward non-kin members, is known to facilitate group living, but attempts to cheat or exploit others. This would be also favored as it brings fitness benefits to the cheater. Recent studies on fairness, a psychological mechanism known to regulate reciprocity and cooperation in humans, in nonhuman animals have provided empirical support for the convergent evolution of a sense of fairness with its link to cooperation. Nonetheless, a lack of studies in closely related species, having different social systems, has led to questions about this hypothesis.

In this dissertation, I presented experiments examining three core questions regarding the evolution of prosociality and its cheater detection mechanisms; 1) proactive prosociality, 2) outcome-based fairness judgment for regulating fair division of resources and cooperation, and 3) behavior-based fairness judgment for regulating reciprocity, by testing a previously neglected semi-solitary primate species, the orangutan.

A prosocial-choice apparatus in which a choice is given to an actor between sharing (prosocial) and not-sharing (selfish) food rewards with a partner, had been employed across all three experiments with only modifications of reward distribution (advantageous vs. disadvantageous food for the actor) for the outcome-based fairness experiment and partner involvement (prosocial vs. selfish partner toward the actor) for the behavior-based fairness experiment. The first experiment testing captive orangutans' ability to voluntarily share foods with their conspecific partners revealed that socially housed captive orangutans do not exhibit a spontaneous (proactive) prosocial tendency toward their conspecifics (compared to the partner-absent control condition). The second experiment tested whether captive orangutans in comparison to captive chimpanzees, display aversive reactions toward disadvantageous outcome inequity and revealed that chimpanzees, but not orangutans, displayed an aversive reaction of

aggressive displays toward their partner when they received an inferior reward, and that dominance influenced the expression of aversion to inequity in a way that aversive reactions were directed to the subordinate, but not to the dominant partner. The third experiment tested whether captive orangutans are able to distinguish between prosocial and selfish partners and reciprocate the received favor or retaliate against the selfish actions by their partners. It was revealed that a male orangutan showed a potential sensitivity to behavioral inequity directed toward familiar human partners, who have previously always provided foods in their daily life, but acted selfishly during the experiment, suggesting an expectancy violation as the most plausible explanation. This male also made higher prosocial choices than the partner-absent control toward a particular female, who showed the highest social interactions in the outdoor exhibit with him, regardless of reward distributions, though it was not statistically significant. Due to the small sample size and weak statistical power, it is hard to confirm whether the observed prosocial tendencies in my experiment reflect the orangutans' capacity to develop prosocial tendency as a function of close social bond or just as an individual characteristic.

In summary, orangutans in my study in general were neither proactively prosocial nor sensitive to outcome inequity, and did not reciprocate received favors from familiar and unfamiliar humans. These results seem to reflect their species-specific sociality of semi-solitary lifestyle. Nonetheless, a male's consistent higher prosocial choices toward a particular female across the experiments and potential sign of retaliation against the selfish action by familiar humans raises the necessity of further investigation. Recent studies on voluntary food sharing, calculated reciprocity, and third-party social evaluation in captive orangutans suggest highly developed social cognitive abilities as well as prosocial tendencies as a function of long-term social bonds or short-term mating associations. Therefore, further studies should follow with orangutans in different populations with different rearing histories to clearly understand the social selective factors, which may drive the evolution and development of prosociality and a sense of fairness in orangutans.