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How do means of measuring contingent cooperation affect whether we observe this in primates?

In terms of animal behaviour, the study of cooperation and prosociality has captivated researchers for many years. Exploring the intricate dynamics of a contingent relationship (defined by Gurven (2006) as acts of giving and receiving amongst members of a social species) not only sheds light on the mechanisms behind their social organisation, but also provides an insight into our own human nature. Researchers tend to focus on observing this in primates due to their complex social structures and the potential for observing cooperative behaviours within their communities. However, studying cooperation in primates presents unique challenges, one of which lies in the means of measuring the phenomenon. Different approaches such as direct observations, experimental designs, and the use of advanced technological equipment each have their own advantages and limitations in capturing contingent cooperation accurately. This essay aims to explore the influence of the different techniques used to detect and interpret contingent cooperation, whilst supporting the position that a combination of said methods should be used to gain a holistic understanding of cooperation in primates, drawing upon supporting research.

Primarily, direct observations are used as a method of studying contingent cooperation in primates, providing valuable insights into their natural social behaviours. Primary research conducted by Cheney *et al.* (2010) exemplifies the advantages of direct observations in studying contingent cooperation. The researchers employed direct observation techniques to study the cooperative hunting behaviour of a group of wild female baboons within their natural habitat. By closely monitoring the hunting strategies and interactions within a baboon troop, Cheney *et al.* were able to uncover patterns of reciprocity and contingent cooperation within the baboons' social network, such as the observation of the females working together to capture prey. They also found individuals who had participated in previous successful hunts were more likely to receive assistance from others in subsequent hunts. This research highlights how direct observations can provide detailed data on the specific behaviours and social interactions that contribute to contingent cooperation, offering a deeper understanding of the adaptive strategies employed by these primates in their cooperative endeavours.

Moreover, studies on cooperative behaviours in hunter-gatherer communities have relied on direct observations of daily activities and social interactions. Gurven *et al.* (2006) conducted an observational study to uncover how contingent relationships exist in food exchange among two groups of forager-agriculturalists; the Ache of Paraguay and the Hiwi of Venezuela. They recorded the number of food sharing events between the Ache hunter-gatherers over a period of 55 sample days, and between the Hiwi foragers for 37 sample days during the wet season. Here, they found that exchange imbalances tend to favour the lower-producing families, close kin, and nearby neighbours. Individuals who shared food were more likely to receive reciprocity in the future, demonstrating the existence of contingencies that promote cooperation within these primate communities.

However, observing contingent cooperation under natural conditions presents several challenges. Cheney (2011) found that a major challenge lies in establishing the casual relationships between specific prior interactions and subsequent altruistic behaviour, particularly without experimental manipulation. Additionally, altruistic acts often differ from one another, for example grooming and

alliance support, which make collected data and results difficult to compare. As a result, the empirically intractable problems label almost any relationship as cooperative. Hence, for results that accurately reflect levels of contingent cooperation we must not only rely on these direct observations, but rather analyse findings alongside data from experiments which utilise alternative methods, such as experimental methods.

Experimental methods offer controlled settings for studying contingent cooperation in primates. One approach involves setting up reciprocal exchange experiments, where individuals are trained to engage in cooperative behaviours such as food sharing. According to research by Brosnan and de Waal (2002), it was determined that capuchin monkeys possess the capabilities to understand and reciprocate cooperation if the approach used is intuitive to them. In their study, capuchins were trained to exchange tokens with experimenters in order to receive a food reward. The researchers systematically manipulated the exchanges, creating conditions of either cooperation or non-cooperation between the capuchins and the experimenters. The results concluded that capuchins demonstrated a strong inclination towards reciprocating with partners who had previously cooperated with them, indicating a clear understanding of contingent cooperation. Experimental designs allow for manipulation of variables, allowing researchers to establish causality between prior interactions and cooperative behaviours. However, it is essential to consider whether artificially induced behaviours in laboratory settings accurately reflect contingent cooperation in natural environments. The artificial nature of experiments may limit ecological validity and fail to capture the full complexity of primate social interactions.

The use of specialist equipment and technological advancements have significantly enhanced the validity of the conclusions we can draw from assessing contingent cooperation in primates. An example of this is the use of advanced tracking systems, such as GPS tracking and radio telemetry techniques. A study by Gilby *et al.* (2013) utilised GPS collars to monitor the movement patterns and social interactions of wild chimpanzees. This technology allowed researchers to gather detailed data on the spatial proximity and affiliative tendencies of individual chimpanzees, providing insights into the contingent nature of their cooperative interactions. Though, the sole use of GPS allows for inaccuracies or lack of depth in research. By combining GPS data with behavioural observations, researchers were able to investigate the influence of prior social interactions on cooperative behaviours, such as hunting and territorial defence. This demonstrates how employing different methods has allowed researchers to discern things about cooperation in primates they might have otherwise overlooked.

Furthermore, the development of sophisticated imaging techniques, such as thermal imaging and remote sensing technologies has enabled researchers to study contingent cooperation in primates from a distance. A further study conducted on wild chimpanzees is that of Barrault *et al.* (2022), who utilised infrared thermography to study the role of audience effects during feeding events. By remotely monitoring their interactions, they were able to identify instances of contingent cooperation and

determine when it is most unlikely to happen, such as feeding in the company of others due to the chimpanzees being in an increased stressful situation. From these results, the research found infrared imaging to be an important complement to access psychological processes beyond observable social behaviours. Hence, this technology has the potential to uncover subtle nuances in primate social interactions and shed light on the underlying mechanisms driving contingent cooperation.

Despite this, there are limitations to consider when using these specialised approaches. Whilst technological advancements such as GPS tracking have proven to be valuable tools in studying contingent cooperation, they also have some disadvantages to be considered. One of the main drawbacks is the potential disruption of natural behaviour caused by the presence of tracking devices. As stated by Tomkiewicz *et al.* (2010), the level of maintenance required for GPS devices may result in excessive disturbance and disruption of normal behaviour displayed by the subject animal. GPS collars or tags can alter the movement patterns of primates, so could potentially influence their social interactions and cooperative behaviours. This, in turn, may lead to biased observations and inaccurate assessments of contingent cooperation and altruistic acts. Additionally, the use of these devices often requires capturing and handling primates which can cause stress and discomfort. Stabach *et al.*'s (2020) study into the effects of GPS collars on the activity and behaviour of scimitar oryx concluded that the tracking devices have the potential to burden their carriers with additional stress. Stress-induced behaviour may not accurately reflect natural cooperative behaviours, thus limiting the validity of the data collected.

The accuracy of thermal imaging can be constrained to only measuring surface temperatures, thereby failing to demonstrate a thorough comprehension of internal physiological changes associated with contingent cooperation. Although, infrared thermography can still provide a unique perspective by capturing thermal patterns associated with cooperative behaviours, offering insights into the physiological responses during social interactions. Therefore, it is essential thermal imaging data is interpreted alongside other behavioural and physiological measures to ensure that the measurements of contingent cooperation in primates accurately represent their natural behaviour and social dynamics.

In conclusion, the means of measuring contingent cooperation in primates play a pivotal role in our understanding of their cooperative behaviours. By utilising a diverse range of approaches, such as direct observations, experimental techniques, and advanced technology, we can enhance the depth and breadth of our understanding. Each method contributes unique insights, shedding light on various facets of primate cooperative behaviours. However, it is important to acknowledge that each method can and is subjected to limitations, such as bias. Though by skilfully integrating these different methods, researchers can navigate these limitations, providing a more holistic understanding of contingent cooperation in primates. Such an approach fosters a richer comprehension of the underlying mechanisms, evolutionary significance, and ecological implications of cooperative behaviours in primates.

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