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Primary Article

Fedurek, P., Slocombe, K. E., Hartel, J. A., & Zuberbühler, K. (2015). Chimpanzee lip-smacking facilitates cooperative behaviour. *Scientific Reports*, *5*(1), 13460. https://doi.org/10.1038/srep13460

Summary:

The study the paper focused on was about how lip-smacking behavior in chimpanzees can affect the different grooming times and reciprocation behavior. Previous knowledge that certain social behaviors in primates are driven by the need for relations in group settings are known, but the specific behaviors are still being identified. This study looked for relationships between the different ways grooming would occur after the groomer initiated it through lip-smacking. Especially at the different aspects of grooming such as length, how often the grooming was reciprocated, body part, and social hierarchy of the chimpanzees. This behavior was studied by using focal animal sampling where one random adult male chimp would be selected and followed between 7:00 to 16:00. Then the grooming and lip-smacking behavior was only recorded in the first 10s of every minute block. They were able to do this for a total of 1038 samples of 10s blocks. They found that lip-smacking occurred in over 65% of all grooming bouts, and that groomers were in front of the groomer. Grooming bouts were also found to be longer and reciprocated if lip-smacking occurred at the start. Overall, the results found that lip-smacking increased cooperation and grooming length between the chimpanzees. The study specifically looked at how chimpanzees used lip-smacking to communicate their needs of grooming to each other. The findings of this article improved the understanding of how lip smacking can be utilized in chimpanzees for their benefit. Lip smacking is important for them as it helps to improve communication for cooperating with others. Additional research can be done on how lip-smacking behavior can form speech-like patterns, as this behavior supports the idea that chimpanzees are actively communicating to get reciprocal behavior. More studies on this behavior can help to provide support for how chimpanzees facilitate cooperative behavior.

Contribution: This article provides new ideas and results on the specific behavior of lip-smacking on cooperative behavior in chimpanzees. The results in the article improves our understanding of the different complex social behaviors that benefit the chimpanzees. Lip-smacking specifically gave insight into how chimpanzees can possibly be communicating and reciprocating behavior within their group. This study gives way for future studies on how chimpanzees actually communicate, and how their behavior can differ based on social interactions with individuals.

Secondary Review Article

Parr, L. A., Waller, B. M., & Fugate, J. (2005). Emotional communication in primates: Implications for neurobiology. *Current Opinion in Neurobiology*, *15*(6), 716–720. https://doi.org/10.1016/j.conb.2005.10.017

Summary:

This article is a review that explores how the brain developed in primates to cope with the increasing demands of group living and social interactions. It looked at several behaviors, specifically the facial expressions, communications, and vocalizations to understand the development of primates in group living. Emotion is thought to be an important factor when it comes to intra- and inter-specific social behaviors that aid in the survival of the species. Facial expressions and vocalizations are the primary means for communicating among primates. Facial expressions are elicited in similar social contexts in different species of primates. Chimpanzees are observed to use the silent bared-teeth face and relaxed open mouth face expressions in very similar social settings to elicit positive behavior between individuals. Despite being vastly different expressions, the common result from the behavior plays a crucial role in forming social relationships between individuals in a social group. Perceiving these signals and behaviors are highly evolved in primates as they have a need for a developed system of interpreting communication from others. With complex social behaviors, come the need for a larger brain size and cognitive skills to effectively deal with the demands of a social group. Behaviors are found to be activated by certain parts of the brain. The expressions of primates caused by complex social groups lead to increased cognitive abilities. This article was an important review because it went into detail of mechanisms that primates utilize to deal with group interactions. It improved the understanding of different behaviors, such as lip-smacking, and how it can be used. Primates show such complex expressions and social behaviors that were driven by the need for increased cognitive functions due to complex social groups. It may suggest that primates use facial expressions to maintain good relations with individuals in their group.

Contribution:

The review highlights how increased demands from complex group living was a driving force for special expressions and communication in primates. Provided an in-depth description of primates facial expressions and behavior, and how they develop valuable social relations between individuals in the group. Although it identifies that production of facial expression helps with social behavior, there is still little that is known about whether primates attach an emotion to individuals that produce these expressions. As a review, this article provided great general information about social behavior in primates, and being able to find other primary literature related to the topic.

Nishida, T., Mitani, C. J., & Watts, P. D. (2004). Variable grooming behaviours in wild chimpanzees. *Folia Primatologica*, 75(1), 31-36. https://doi.org/10.1159/000073429.

Summary:

This study looked at how grooming behaviors in two various wild chimpanzees populations can be different, and why they developed that way. Previous knowledge about the regional differences in grooming, feeding, and social behaviors are known about the populations. However, this study adds on to that list of observations by looking at locale-specific grooming patterns of the population. The two populations looked at in this study were the chimpanzees at Ngogo, Uganda and Mahale, Tanzania study sites. They studied only the adult and adolescent males in the population of about 150 chimpanzees for both study sites, and observed and recorded their grooming behaviors over a period of 22 days. It was found that one behavior, known as social scratching, occurred in 86% of adult males in the Ngogo unit and appeared to be an important behavior among the individuals. Comparison between the Ngogo and Mahale groups showed that there were variations in the length of scratch, and if the adult males preferred either male or female chimpanzees. It was also found that lip-smacking was an important sound used when grooming other individuals. Comparison between the two study sites showed that chimpanzees at Ngogo produced a different type of sound during grooming, than those compared in the Mahale study site. These results in the study show that there are significant differences between groups of chimpanzees, but they all seem to have similar behaviors during grooming sessions. Observations of these chimpanzees gave finding to new behaviors and how they are utilized for grooming. Additional research can be done to explain these differences, how behaviors are developed, and whether they are passed on socially through learning.

Contribution:

This article adds on to previous knowledge of different behaviors in chimpanzees while they are grooming, feeding, and socially interacting. The results they provide show an increased understanding of the types of behaviors during grooming, and how they might have developed. They allow for future studies on how social behavior might be passed on through learning and observation. The article is important to see the variations in behaviors and how we can study them to understand how they develop.

Watts, D. P. (2016). Production of grooming-associated sounds by chimpanzees (*Pan troglodytes*) at Ngogo: Variation, social learning, and possible functions. *Primates*, *57*(1), 61–72. https://doi.org/10.1007/s10329-015-0497-8.

Summary:

This study was looking at specific behaviors that chimpanzees produce while grooming and how that can lead to variation, learning, and functions among the individuals. Previous studies have observed various primates, specifically, chimpanzees and how they utilize vocalizations during social interactions. They have looked at many different types of behaviors, such as calls, drumming, and ground slaps. This study focuses on splutters, teeth chomps, and lip smacking/popping in the group of chimpanzees at Ngogo study site. They looked at how specific behaviors are developed in the individuals, and how such dependence on sounds can be important for social learning and relations. The wild chimpanzee population at Ngogo study site in Kibale was the observation focus for this study, with around 200 chimpanzees. Data collected over 22 months using focal samples of adult and adolescent males grooming sessions. They observed the length of grooming sessions above 30s and if sounds initiated the grooming. It was found that over 77% of individuals either spluttered or teeth chomped or both, and over 60.5% lip smacked during grooming. It was observed that the sounds produced were increased with increasing grooming length, and with the grooming was bidirectional. Grooming bouts were significantly longer when initiated with sounds such as lip smacking or spluttering, than without sounds. The findings of this study showed that sound production is at least voluntary by the chimpanzees. It supported the idea that chimpanzees utilize behaviors of producing sounds to communicate to other individuals about their needs especially during grooming sessions. However a lot is still unknown about the motivation of producing sounds, and if they really need to in order to maintain social relations in the group. Additional research can be done to improve the understanding about the development of these behaviors.

Contribution:

This article builds on the observations of sound producing behaviors of chimpanzees specifically during grooming. It involves a more in-depth research on sounds such as spluttering, lip-smacking, and teeth chomping and how they benefit the chimpanzee during grooming and building social relations. Much is still unknown about the exact motivation and development of this behavior. This article is important to understand and give more support to chimpanzees producing sounds during grooming. It improves understanding of the dependence of these sounds as chimpanzees engage in their grooming sessions.

Gomes, C. M., Mundry, R., & Boesch, C. (2009). Long-term reciprocation of grooming in wild West African chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1657), 699–706. https://doi.org/10.1098/rspb.2008.1324

Summary:

This study is looking at if grooming is reciprocated in wild chimpanzees and the mechanisms that lead to this behavior. Previous knowledge in this field shows that many primates seem to engage in behavior that represents reciprocity among the individuals, whether it be with kin or non-kin. However, not much is known about if chimpanzees can keep track of their previous interactions, and if they better reciprocate on a short term or long term basis. This study looks at how grooming in chimpanzees is an ideal behavior for judging reciprocation, as it can be easily observed whether it is unidirectional or bidirectional in a given time. The study conducted focal sampling from 2003 to 2006 on a group of 44 chimpanzees in Cote d'Ivoire. They observed the frequency of grooming sessions, and kept track of which chimpanzees reciprocated and such through the collection. It was found that out of all the grooming sessions recorded, only around 32% were bidirectional or reciprocated, meaning most of the time the chimpanzees did not reciprocate grooming. However, within the reciprocation of grooming observations, it was found that most of the bouts occurred on individuals who were familiar due to the frequency of grooming each other over a long period of time. This suggests that chimpanzees were able to keep track of their grooming interactions over a longer time period. This study significantly improves the understanding of how chimpanzees could reciprocate through grooming, and how they keep track of previous interactions. The study gives some proximate mechanisms such as the animal having a positive emotional attitude to an individual, which increases the likelihood of reciprocation. However, much is still not known about the mechanisms that allow chimpanzees to keep track of grooming and engage in reciprocal behavior.

Contribution:

This article provides new research into reciprocation behavior in chimpanzees specifically during grooming sessions among individuals. It provides new information on the mechanisms that give chimpanzees a reason to engage in reciprocity and keep track of previous grooming interactions. Many proximate mechanisms were introduced in this article to give support to the behavior in chimpanzees. However, further studies can be done to add onto the motivation for chimpanzees to engage in reciprocal behavior. This article was important as it provided more information on grooming behavior in chimpanzees and how it benefits them in social interactions.

Allanic, M., Hayashi, M., & Matsuzawa, T. (2020). Investigating the function of mutual grooming in captive bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*). *Folia Primatologica*, *91*(5), 481–494. https://doi.org/10.1159/000506308

Summary:

This study is comparing how mutual grooming is engaged among bonobos and chimpanzees, and the reasons for that behavior. Previous studies have found that chimpanzees' mutual grooming was frequent among chimpanzees, but not a lot is known about why and how it compares to other primate species. This study adds on to the observations of chimpanzees, and compares it to bonobo grooming behavior to greater understanding of the mechanisms of mutual grooming. They observed captive bonobos and chimpanzees at Kumamoto study site at Kyoto, with 6 bonobos and 7 chimpanzees. They collected the data over 61 days for bonobos at 43 days for chimpanzees, mostly doing focal animal sampling of the grooming behavior of each individual. A total of 153 grooming bouts was observed, around 41% of these were reciprocated for both species. It was found that grooming bouts with mutual grooming were significantly longer than without mutual grooming. The study found that grooming did not seem to be caused by the need for strong dyadic social bonds. However, mutual grooming can be used as an indicator for social bonds among individuals. This study expanded the knowledge of the motivations for chimpanzees and bonobos to engage in mutual grooming. They found that mutual grooming mostly served to maximize short-term benefits for the animals, such as longer grooming, and increasing the reciprocity while grooming. This suggests that reciprocal grooming is used to drive cooperative social interaction to gain immediate benefits for the individuals. It was found that both bonobos and chimpanzees exhibit similar mechanisms for mutual grooming. However, a lot is still unknown about the differences among kin, sexes, and social hierarchy when it comes to grooming. Future studies can look more into these details to give a more complete mechanism for mutual grooming.

Contribution:

This article provides more detail into the reason why chimpanzees seem to engage in mutual grooming much more than other primate species, and compares the observation with bonobos. It supports ideas from previous findings about the benefits of mutual grooming and the mechanisms behind the behavior. It adds on to the knowledge and provides new support for why grooming is used to give immediate benefits to the primate species. This article is important because it gives a better explanation behind the mechanism, and provides a comparative study that adds to the understanding.

Jensvold, M. L. A. (2008). Chimpanzee (*Pan troglodytes*) responses to caregiver use of chimpanzee behaviors. *Zoo Biology*, 27(5), 345–359. https://doi.org/10.1002/zoo.20194

Summary:

This study is looking at how caregivers that utilize species-specific behaviors in chimpanzees can affect the relationship they build together. Previous observation on other animals has been done before and found that it can increase the animals' quality of life, even on chimpanzees. This study goes more into depth at looking at how chimpanzees interact with the caregivers when they either have species-specific behavior or regular human behavior. Three male chimpanzees were the primary subjects of this study for the human caregivers who would interact with them, at the Bush Gardens Zoo in Tampa. The caregivers were trained using a video that showed all the different types of chimpanzee behavior, and they were able to replicate them. The caregivers either performed chimpanzee behavior conditions (lip-smacking, grooming noises, etc.) or human behavior conditions randomly during their interactions throughout the day for the duration of the study. It was found that on average an interaction was 15min when the caregiver was engaging in species-specific, and 10 min when they were just doing normal behavior. The study found that all the chimpanzees were significantly more interactive with the caregiver during species-specific behavior than normal behavior. The study expands on the idea that engaging in behavior that is friendly and familiar to chimpanzees drastically improves the relationship between them and leads to a better quality of life for the chimpanzees. This suggests that certain behaviors are important to chimpanzees and they are able to recognize and learn that they are beneficial to social relations. However, much is still unknown about how these behaviors are important to the chimpanzees, and how they develop them to get better communication among individuals. Future studies can look more into different behaviors and how they interact with each other.

Contribution:

This article provides new knowledge and observations into how chimpanzees interact with caregivers when they are engaging in species-specific behavior. This helps to better understand the types of behaviors that are important to chimpanzees, and how they can recognize and communicate their needs. This study supports the idea that engaging in species-specific behavior improves the relationship with the chimpanzees and increases their quality of life. This is important as it gives an indepth look into how chimpanzees interact with humans and how this can be used to study their behaviors in the wild.

Bard, K. A., Dunbar, S., Maguire-Herring, V., Veira, Y., Hayes, K. G., & McDonald, K. (2014). Gestures and social-emotional communicative development in chimpanzee infants: Gestural development in chimpanzees. *American Journal of Primatology*, 76(1), 14–29. https://doi.org/10.1002/ajp.22189

Summary:

This study focused on the early development of behaviors in infant chimpanzees. Previous studies looked at certain aspects of development but have limited information on these gestures in chimpanzees. This study specifically adds on to this knowledge by looking at not only the form of the development, but also the communicative function behind it. The study observed how behaviors that develop in early infants all seem to have a communicative meaning for them. Seventeen infant chimpanzees were given responsive care from their birth to 52 weeks of age, at Yerkes National Primate Research Centre. This means that each caregiver engaged in species-specific behavior at the time of development that naturally occurs in the wild. Through this care they observed and recorded the milestones of each developmental behavior for each of the infant chimpanzees. They observed the timeframe of the development of certain behaviors. It was found that engagement of the behaviors, such as tickle, chase-play, and grooming, was much earlier than initiations of these behaviors themselves. For grooming, the infants started to engage around 4 weeks, initiate behavior at 19 weeks, and request at 38 weeks of development. Many of the behavioral components of grooming, such as facial movements and vocalizations, were observed to be developed later during the initiation stage. The findings show that behaviors develop in chimpanzees early on in infancy, first engaging, initiating and then requesting the behavior. The study found important support for a communicative meaning behind all the behaviors that develop. This gave a better insight into how behavior is developed, and that there are several processes for development in chimpanzees. However, a lot is still unknown about these and other behaviors in chimpanzees, and the meaning behind their development. Future studies can focus on these different types and the communicative features behind them.

Contribution:

This article adds new knowledge and ideas on how early behavior develops and the purpose behind it in infant chimpanzees. This study gives a better understanding of the communicative function of all early developments of social behavior in chimpanzees. Their study supports the idea that development of behaviors in chimpanzees all seems to come from a need to communicate even as infants. This study is important because it give an idea of the mechanism for why certain social behaviors developed in chimpanzees, and how they benefit the animals as they develop.

Secondary Article:

Burrows, A. M., Li, L., Waller, B. M., & Micheletta, J. (2016). Social variables exert selective pressures in the evolution and form of primate mimetic musculature. *Journal of Anatomy*, 228(4), 595–607. https://doi.org/10.1111/joa.12440

Summary:

This article is a review that looks at the influence of social variables on the adaptations of mimetic musculature specifically in primates. The review focused on the morphological and physiological examples to show how social pressures may lead to the adaptations of facial expressions in primates. Social variables here include the group size, dominance style, and mating systems. Two case studies were looked at in this review, to present potential influences of social behavior on the adaptive morphology in primates. The morphology of muscles around the external ear, and the oris muscle are seen to be certain muscles that are used in facial expressions in primates. Qualitative observations were presented in this review to show the specific muscle distributions in chimpanzees that can be related to the production of sounds and their facial expressions. Visual communication through facial displays are the primary ways for social communication especially in the proximate level. Primates seem to have adapted their neurobiology in a way that has increased their brain size in regions associated with facial expressions. The review showed that species living in complex social groups tend to have more facial nerve neurons that are related to control of their facial muscles. These findings may suggest a link among the morphology of the face muscles, and the behavioral facial expressions made by primates. It suggests that the improved understanding of facial musculature can lead to the comprehension that primates have adapted in social conditions for their benefit in creating social bonds and improving fitness. Future studies more into the morphology and physiological link and expand the knowledge of how primates evolved social behavior.

Contribution:

This review article highlights how facial expressions in primates are controlled by their adapted musculare due to social pressures in their environment. Improved the understanding of how facial muscles are distributed in primates, and how that adaptation is related to improving social relations and behavior in their primate groups. However, still a lot is unknown about the mechanisms that led to this adaptation in primates, and how beneficial it is for the individuals. As a review, this article provided a lot of knowledge on different morphological adaptations in primates that has led to increased social behavior.