

**Biological market behaviour as a model for reciprocal altruism in wild white-handed gibbons  
*Hylobates lar*; a broader look at Khao Yai National Park**

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**Introduction**

Reciprocal altruism has been a much debated topic in animal behaviour since the initial release of Darwin's theories (Darwin, 1871). Reciprocal altruism is one part of the theory describing co-operative actions between animals; specifically it is the exchange of costly acts between individuals in which one individual benefits initially and later on the other individual receives some sort of benefit (Brosnan and de Waal, 2002). It is important to note the temporal difference in when benefits are received, as this is what distinguishes reciprocal altruism from mutualism, where benefits are received at the same time in both parties (Holland and Bronstein, 2008). The idea of reciprocal altruism is interesting in the sense that involves some sort of seemingly detrimental act by one party, which is not what is expected by classical Darwinian thinking, where all actions seek to benefit a given organism in some way (Brosnan and de Waal, 2002).

Biological market theory seeks to expand on the concept of reciprocal altruism by considering the costly acts exchanged as commodities that are traded within a social market (Noë et al., 1991). In this sense, an animal will trade one behaviour that does not initially benefit itself to another. In return, the animal receiving the trade will reciprocate the benefits, either by providing the same actions back or interchanging them with a different, yet still beneficial action (Noë and Hammerstein, 1995). The idea of a biological market states that in the absence of force, there is a mechanism in place to display value through the offering of services or behaviours, called commodities. Also, as the rarity the commodity being offered increases, there is also an increase in the demand for commodities being returned (Barelli et al., 2011).

The exchange of grooming has been well documented as a commodity often traded in primate communities. It has benefits such as parasite removal (Reichard and Sommer, 1994) and costs to the animal grooming in terms of time it could be spending doing something else (Cords, 1995). Grooming in primates is often used as a commodity traded for mating opportunities, often in species where males cannot physically impose sexual advances (Barelli et al., 2011; Plavcan and van Schaik, 1997).

The aim of this study is to expand upon previous studies conducted on wild white-handed gibbons (*Hylobates lar*) at Khao Yai National Park, Thailand by observing a larger sampling size. Previous studies have focused only on the determination of grooming as commodity by comparing the amount of time males groom females to the reproductive state of the females (Barelli et al., 2011). This study would expand on this by looking at the structure of groups of gibbons, as groups will typically be either single-male or multi-male (Barelli et al., 2008a). Competition to find a mate in single-male groups would

be relatively low compared to that of multi-male groups, so it would be expected that multi-male groups would have a greater exchange of commodities. Specifically, there would be an increase in the amount of time spent grooming during periods in which females are reproductively active.

To further investigate the role of commodities, the exchange of grooming should as be compared to some other commodity aside from sexual selection as there may be other factors which influence that (Barelli et al. 2011). It has been documented that female gibbons control the food supply in gibbon groups, as they are often seen eating alone from the group or leading the group to food sources (Barelli et al., 2008b). If grooming is in fact a commodity being exchanged, then the amount of time males groom females should also increase when food supplies are relatively scarce. It would be expected then, to see males eating with normally lone females or being near the front of the pack when being led to food.

The idea of a biological market is still relatively new, but it provides important insights into group dynamics. It looks at how resources are portioned within a species and the value a species places on a resource. By learning how individual exchanges occur between animals, we can further ascertain how animals maintain group environments and why living in groups is beneficial.

## **Methods**

This study seeks to expand on previously conducted studies in the area of Mo Singto–Klong E-Tau in Khao Yai National Park, Thailand, so there are already well established methods for data collection. Specifically, the methods outlined by Barelli et al. (2011) would be applied. Groups of gibbons would be observed with a distinction between single-male and multi-male groups being made. Within the groups, female gibbons would be the focal point of observation. Female gibbons would be observed from dawn to dusk with all sexual activity and grooming encounters recorded. To determine whether a female is reproductively active, fecal matter would be collected and examined as outlined in Barelli and Heistermann (2009) and then correlated with time spent grooming. In addition to methods outlined in Barelli et al. (2011), observations of feeding behaviours of females with emphasis on their encounters with males while feeding, would be recorded. The amount of food available would be recorded as well as how much is consumed by which members of the group.

## **Results**

If grooming is a commodity traded for mating opportunities, then the amount of time spent grooming should increase when females are most reproductively active. If the commodity is exchanged, there should be an increase in the amount of copulations received by a male. Also, males should spend more time grooming females than females spend grooming males. When comparing the grooming patterns of single-male groups to multi-male groups, male's in a single male group should spend less time grooming and would groom over-all, less females. Males in a multi-male group should then spend more time grooming than males in a single group and should groom a larger variety of females. If grooming is not an important factor in determining mating opportunities, then males of both single-male and multi-male groups should groom the same amount and receive the same amount of copulation.

With respect to the exchange of food resources, females should receive more grooming when there is a scarcity of food. Males who do the most grooming should proportionately receive more food than males who do less grooming. It would also be expected that males who groom females more will be able to access a food source before a male that grooms females less. Also, males that groom the female that most often leads the group to food sources will have a greater access to food than other males. If there is no exchange of commodities, then males who do the most grooming will not be among the first to access food nor will they receive any more food than males who do relatively low amounts of grooming.

## **Discussion**

Previous studies have found a strong link between the exchange of grooming with other goods, but such studies have often also found that when males increase grooming activity of females, females also increase grooming activity of males. This is why it is important to include the exchange of grooming for access to food, for any correlation between food access and grooming habits cannot be explained simply by mutual reciprocation (Barelli et al. 2011; Brosnan and de Waal, 2002). As it has been shown that females have first access to food sources (Barelli et al., 2008b), any indication of an occurrence where a female that should have priority access to food but doesn't could be considered an act of trading commodities if sometime before that a male had groomed the female.

Studies of gibbons in this area having been lacking in sample size. By increasing the sample size to include more groups of gibbons, with attention to increasing the amount of multi-male groups, there should be a clear distinction between males of different groups. Males of single-male groups will spend less time grooming because they are under less competitive pressure to find a mate. Their reproductive success is virtually guaranteed so they should invest their time in other behaviours aside from grooming females. Males from multi-male groups will spend considerably more time grooming females as they must encourage the female to find value in themselves. Within multi-male groups, males under more competitive pressure to display their worth to females, so they will spend more time grooming than males from single-male groups. However, multi-male groups have a tendency to have primary and secondary males (Barelli et al., 2008a), where primary males copulate more than secondary males. Therefore, secondary males should spend more time grooming than primary males because they are naturally least likely to be selected and need to influence the decision of females more.

Since gibbons are a sexually monomorphic species (Plavcan and van Schaik, 1997), males do not have much control over the behaviour of females. Therefore, commodities such as food and grooming are more so controlled by supply and demand as predicted by biological market behaviour (Barelli et al., 2011). There is little literature on the benefits analysis of grooming interchanged for other commodities. By examining the association of food allocation with grooming patterns, the theory of biological market behaviour can be further attributed by explaining the benefits received by females in commodity exchange. Also, this study will help to clarify the gradient between supply and demand of grooming behaviour and add more literature to the limited supply on biological market behaviour.

## **Literature Cited**

- Barelli, C. & Heistermann, M.** 2009. Monitoring female reproductive status using fecal hormone analysis and preliminary data on patterns of genital swellings in relation to female cycle stage in captive and wild white-handed gibbons (*Hylobates lar*), S.M. Lappan, D. Whittaker, T. Geissmann, Editors , *The Gibbons: New Perspectives on Small Ape Socioecology and Population Biology*, Springer, New York, 313–325.
- Barelli, C., Reichard, U.H. & Mundry, R.** 2011. Is grooming used as a commodity in wild white-handed gibbons, (*Hylobates lar*)?. *Animal Behaviour*, **82**, 801-809.
- Barelli, C., Heistermann, M., Boesch, C., and Reichard, U.H.** 2008a. Mating patterns and sexual swellings in pair-living and multimale groups of wild white-handed gibbons (*Hylobates lar*). *Animal Behaviour*, **75**, 991–1001
- Barelli, C., Boesch, C., Heistermann, M. & Reichard, U.H.** 2008b. Female white-handed gibbons (*Hylobates lar*) lead group movements and have priority of access to food resources. *Behaviour*, **145**, 965–981.
- Brosnan, S.F. & de Waal, F.B.M.** 2002. A proximate perspective on reciprocal altruism. *Human Nature*, **13**, 129–152.
- Cords, M.** 1995. Predator vigilance costs of allogrooming in wild blue monkeys. *Behaviour*, **132**, 559–569.
- Darwin, C.** 1871. *The Descent of Man and Selection in Relation to Sex*, Modern Library, New York
- Holland, J.N. & Bronstein, J.L.** 2008. Mutualism. *Encyclopedia of Ecology*, 2485-2491.
- Noë, R. & Hammerstein, P.** 1995. Biological markets. *Trends in Ecology & Evolution*, **10**, 336–339.
- Noë, R., van Schaik, C.P. & van Hooff, J.A.R.A.M.** 1991. The market effect: an explanation for pay-off asymmetries among collaborating animals. *Ethology*, **87**, 97–118.
- Plavcan, J.M. & van Schaik, C.P.** 1999. Intrasexual competition and body weight dimorphism in anthropoid primates. *American Journal of Physical Anthropology*, **103**, 37–68
- Reichard, U.H. & Sommer, V.** 1994. Grooming site preferences in wild white-handed gibbons (*Hylobates lar*). *Primates*, **35**, 369–374.

