

WEDNESDAY, 29 May 2019

WELCOME NOTES

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Roman Wittig

Lecture Hall, MPI EVA

Chimpanzees of the Taï National Park, Côte d'Ivoire: The Taï Chimpanzee Project

Roman M. Wittig

The Taï chimpanzees inhabit the Taï National Park (Côte d'Ivoire), the last remaining area of primary rain forest in West Africa, and home to a viable predator population. Observations of the chimpanzees over the last 40 years revealed, amongst others, extraordinary tool use, cooperation during hunting and cultural variation between neighbouring communities. One of the most puzzling social differences to other wild chimpanzee populations are their mixed sex association and bonding patterns as well as female involvement in cooperation. Here I will present the pattern of sociality in Taï chimpanzees and discuss potential factors that might have constituted these differences.

Chimpanzees of the Budongo Forest, Uganda

Catherine Hobaiter

The Budongo Forest lies in the Rift Valley in Northwestern Uganda and contains an est. 600 East African chimpanzees. Following early observations in the 1960s, continuous study of chimpanzee behaviour started in 1990. Long-term research has focused on questions of social organisation, communication, and tool-use in the neighbouring Sonso and Waibira communities. Noteworthy for their apparently species-unique absence of stick tool-use, Budongo chimpanzees show a rich repertoire of leaf-tools, which provided the first direct evidence for social learning in wild apes. The use of innovative field-experiment methodologies has allowed the exploration of wild chimpanzee cognition to be grounded in socio-ecological context.

Biology and behavior of West African chimpanzees (*Pan troglodytes verus*) in a semi-arid environment at Fongoli, Senegal

Jill Pruetz

The chimpanzee group at Fongoli, Senegal has been studied since 2001 and remains the only community thus far habituated in a semi-arid environment. Apes in this savanna-woodland mosaic exhibit behaviors that are unique or rare in other chimpanzees. Fongoli apes adjust to high heat and scarce water stress by being active at night, using caves, soaking in water pools and resting extensively during dry season months. Female chimpanzees, in particular, focus hunting behavior on *Galago* prey, using tools to acquire these nocturnal primates. Similar to other West African chimpanzee communities, Fongoli apes often range in cohesive parties and as a single party at times. They exhibit shorter inter birth intervals than chimpanzees at most other sites, and resume postpartum estrous cycles more quickly.

Long-term studies of the chimpanzees of Gombe National Park, Tanzania

Anne Pusey

Since the initiation of her path-breaking work in 1960, Jane Goodall has supported and maintained the systematic and continuous study of the Gombe chimpanzees. Longitudinal observation of more than 340 individuals in two communities has allowed us to characterize many aspects of chimpanzee biology including life history patterns, social organization, inter-community relations, dispersal patterns, hunting, effects of ecological change on behavior, and sex differences in dispersion and sociality, dominance hierarchies, reproductive strategies, and social development. Exciting recent discoveries include evidence of discrimination of paternal kin, cultural differences between communities, and genetic differences in susceptibility to disease.

Chimpanzee Sociality and Ecology in the Central African Forests of the Goulougo Triangle

David Morgan & Crickette Sanz

Comparisons between wild chimpanzee communities indicate a high degree of social variation can exist depending on local environmental circumstances. To better understand the range of social flexibility in *Pan*, we studied attributes and dimensions of associations within the social network of the Moto community in the Goulougo Triangle, Republic of Congo. We relate these findings to specific characteristics of central African lowland forest and coexistence with western lowland gorillas. Against this backdrop, we also discuss relevant discoveries about population dynamics and disease made at the site over the last 20 years.

Preliminary Observations of Chimpanzees in a Mosaic, Miombo Woodland

Alexander K. Piel, A. Crunchant, C. Giuliano, F.A. Stewart

Wild chimpanzees have been studied for over half a century in Africa, mostly in the rich tropical forests that characterise the central belt of the continent. Reconstructions of Pliocene habitats are characterised as mosaic landscapes, however. By studying chimpanzees that live in a similar contemporary (dry) habitat, we are able to observe potential environmental challenges that early hominins might have faced, and investigate behavioural responses made by an extant ape. I summarise preliminary findings from recent research and contextualise these results in broader chimpanzee and overall ecosystem conservation, as well as human evolutionary processes.

Studies on chimpanzees in the Kalinzu Central Forest Reserve, Uganda

Chie Hashimoto & Takeshi Furuichi

Studies on chimpanzees in the Kalinzu Forest began in 1992. Two neighboring groups, the M and S groups, have been well habituated and all members are individually identified. As in the other study sites in Uganda, the density of chimpanzees in the Kalinzu Forest is as high as 1.76 animals/km², and interbirth interval is as short as in bonobos. The main study group consists of 90 to 100 animals including 15 to 19 adult males. With such a large number of males, when an alpha male or allies of a few high-ranking males fail to monopoly an estrous female, extremely promiscuous mating occurs with very high frequency with most of the male members in the party participating.

The Kibale Chimpanzee Project at 32

Martin N. Muller

Kanyawara chimpanzees are extraordinarily ordinary. Their community size (~55), population density (1-2/sq km), birth intervals (~64 months), body size, food abundance, and hunting rates fall near the mean, across sites. They have escaped the most ruinous epidemics, enjoying low mortality and modest population growth since observations began in the early 1980s. Kanyawara is unique among field sites, however, in having accumulated >40,000 urine samples since 1998, alongside detailed behavioral observations, including >50,000 aggressive interactions. These allow us to study longitudinal relationships between physiology and social behavior on an unprecedented scale, including sexual coercion, female competition, and male politics.

40 years of TCP

Christophe Boesch

WAR AND PEACE IN THE TAÏ CHIMPANZEE FOREST:

RUNNING A LONG-TERM CHIMPANZEE RESEARCH PROJECT

The Taï Chimpanzee Project (TCP) was initiated 1979 to obtain data on rainforest living chimpanzees, as only chimpanzees in woodland savanna of Gombe and Mahale National Park were known. Introducing ecology into the discussion about chimpanzee behavioral diversity, we identified human poaching and leopard hunting as important ecological pressures. Over 40 years, the TCP overcame two civil wars, recurrent poaching, and the dramatic impact of Ebola, anthrax, and respiratory diseases. Fortunately, the project habituated three neighbouring chimpanzee communities, integrating many local students and assistants to ensure continuity of data collection and the security of chimpanzees, even in times of extreme political instability. Taï National Park has become an island within a huge cocoa and coffee plantation, which the chimpanzees and the TCP survived thanks to the extreme dedication of local and international project members, a project-specific law enforcement program, a complete health monitoring program, and the support of local human populations. Taï chimpanzees have become famous for their nut-cracking behavior, high level of cooperative hunting, and extensive cultural diversity.

THURSDAY, 30 May 2019

The Loango Chimpanzee Project

Simone Pika & Tobias Deschner

We provide an overview on the research of the Loango Chimpanzee Project, Gabon. The site is ecologically very distinct from other long-term chimpanzee sites, consisting of a mosaic of different habitat types varying from marine, coastal lagoons, mangrove swamps, coastal forest, secondary and primary forest to open savannah. We will present data on home range and community size, as well as on ranging patterns and party composition. Furthermore, we report on distinct behavioral elements, which seem to differ from those reported for other populations. Finally, we will describe patterns of tool use and predation, including the predation on tortoises.

Japanese primatology and the long-term studies of chimpanzees in Mahale

Michio Nakamura

Field studies of great apes by Kyoto University researchers led by Kinji Imanishi and Jun'ichiro Itani started in the late 1950s. They first surveyed gorillas in Congo but soon shifted the target to chimpanzees in Tanzania. After several years of struggling to find a suitable place for the long-term research, Toshisada Nishida finally habituated chimpanzees at Kasoje area in the Mahale Mountains in 1965. Since then, many researchers and students continued the study and maintained the research project. I will introduce major findings and recent study topics at Mahale, as well as uniqueness of the environment and social structure.

The Ngogo Chimpanzee Project

David Watts

The Ngogo Chimpanzee Project (Kibale National Park, Uganda) started in 1995. Research has focused on social dynamics, mating and reproductive success, feeding ecology, behavioral endocrinology, hunting and meat eating, intergroup aggression, and other topics. The large size of the Ngogo community makes Ngogo data particularly valuable for comparison with those from Kanyawara (also in Kibale) and elsewhere. They show that in favorable ecological circumstances and in the absence of major anthropogenic disturbance, community size can exceed 200 individuals, survivorship can be surprisingly high, female eastern chimpanzees can be highly gregarious, and demography can have many effects on behavioral ecology.

The Pan African Programme: The cultured chimpanzee

Hjalmar Kühl

For understanding the influence and importance of ecological conditions on the diversification of chimpanzee populations a larger number of sites than the currently existing long-term research projects is needed. To address this limitation we launched the Pan African Programme (PanAf), for which we collected standardized information on resource availability, demographic and social structure, behavioural and cultural traits at 39 locations. We will present the overall PanAf concept and first results, including the discovery of new behaviours, drivers of behavioural diversity, variation in social structure and give an outlook to the potential of the PanAf in complementing long-term research on chimpanzees.

The evolutionary road to syntax

Klaus Zuberbühler

Syntax is habitually named as what sets human language apart from other communication systems, but how did it evolve? I discuss three empirical approaches to the problem; evolution by computational capacities, evolution by structural flexibility and evolution by event categorisation. I will evaluate relevant data for the different hypotheses and propose future research.

Why Does the Chimpanzee Vocal Repertoire Remain Poorly Understood? And What Can Be Done About It.

Catherine Crockford

After decades of research, the origins of human speech remain little understood. One undoubted problem is that the vocal repertoires of humans' closest living relatives, the apes, remain poorly described. I posit several reasons why a comprehensive analysis of the chimpanzee vocal repertoire has not yet been completed, in spite of 45 years of research, and what can be done to remedy this situation. Using a cross-site perspective I examine call specificity, contexts of usage, and potential call functions.

Why do male chimpanzees produce food-associated calls?

Katie Slocombe

Male chimpanzees commonly produce food-associated calls on arrival at feeding sites and when others join the feeding party. I will present observational data and field experiments from chimpanzee communities in Kibale and Budongo forests, Uganda, that were designed to probe the social and ecological variables that influence the likelihood of males calling and the structure of their calls. Similarities and differences to investigations of food calling behavior in the Tai communities will be explored.

Conserved vocal production and rapid auditory learning in Old World monkey communication

Julia Fischer

A prerequisite for conventionalized communication in the auditory-vocal domain is flexibility in both vocal production and comprehension of sounds. Studies on potential vocal learning and variation between species in the genera *Chlorocebus* and *Papio* revealed that within genera, the vocal repertoires were structurally highly similar. A field experiment that comprised of the presentation of a novel aerial threat (a drone) with the subsequent playback of the sound of the drone showed that green monkeys, *Chlorocebus sabaues*, immediately responded with orienting responses, including scanning of the sky and running into cover. In conclusion, the structure of the vocalizations appears highly conserved, while comprehension learning is rapid and open-ended. I will argue that vocal production learning needs to be further decomposed to reconcile some of the contradictory findings on nonhuman primate vocal learning that emerged over the last years.

SUMMARY & DISCUSSION: Communication Session

Klaus Zuberbühler

Social Cognition in Chimpanzees and other Primates

Robert Seyfarth

This session focuses on social cognition, defined as individuals' knowledge of their own and other animals' social interactions and relationships. Comparisons between apes and other primates are of special interest because, when compared with Old World monkeys, chimpanzees have larger brains, a proportionately larger prefrontal cortex, make tools, often engage in broad-scale coordinated action, and live in social systems that would seem to favor skills in representing other individuals' mental states. Nonetheless, it is presently unclear exactly how chimpanzees' knowledge

of other animals' relationships differs from that in monkeys. Data from human children offer a useful comparative perspective.

Socio-cognition in Pan: a comparative analysis of cooperation around a simulated danger

Cédric Girard-Buttoz & Patrick Tkaczynski

The Interdependence hypothesis states that the cognitive component of human extraordinary in-group cooperative abilities evolved in contexts where humans needed to coordinate collective actions to achieve a common goal. We tested this hypothesis using a snake model presentation paradigm allowing the ape to express cooperative act, namely produce alarm calls to inform others about the threat. We compared the efficiency of the information transfer and the socio-cognitive triggers of alarm call production in three wild populations of *Pan* with strong differences in the degree of group-level collaboration: Western Tai chimpanzees, Eastern Budongo chimpanzees and Luikotale bonobos.

Lab cognition going wild: field experiments on vervet monkeys

Erica van de Waal

The social brain hypothesis proposes that complex social environments selected for advanced cognitive abilities in certain classes of vertebrates, including primates. Advances in testing and refining the hypothesis will depend crucially on our ability to link the ecology of species to social decision making and underlying cognitive processes. Therefore, we need to study animals in their natural habitat. I will present field experiments on vervet monkeys testing physical cognition, spatial memory, third party relationship knowledge as well as social learning strategies to highlight the feasibility to study cognition under field conditions.

Human Cognition

Daniel Haur

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SUMMARY & DISCUSSION: Cognition Session

Robert Seyfarth

Animal cooperation

John C. Mitani

Cooperation, behavior that has positive effects on the fitness of others, appears to occur throughout the animal kingdom and features prominently in the lives of chimpanzees. Yet cooperative behavior creates a puzzle, as it is difficult to explain by natural selection, the primary agent of evolutionary change. I set the stage to the session on Cooperation in this Introduction by briefly reviewing theoretical explanations for cooperation and highlighting the role that studies of chimpanzees have played in increasing our empirical understanding of this central problem in animal behavior.

What promotes non-kin cooperation in the Tai Forest chimpanzees?

Liran Samuni

Why cooperate with non-kin when there is no immediate reward to actors, is a central question in the field of evolutionary biology, as it is difficult to explain by mechanisms of natural selection. I address this question by investigating some of the underlying mechanisms that may facilitate contribution to cooperative acts in male and female chimpanzees of the Tai Forest. Chimpanzees exhibit some of the most remarkable examples of non-kin cooperation in non-human animals, during border patrols, intergroup encounters and hunting. I present data on behavioural and physiological mechanisms that potentially influence participation and stabilize cooperation during such group cooperative acts in chimpanzees.

Cooperation in Ngogo chimpanzees

Kevin Langergraber

Chimpanzees cooperate to compete with other members of their group for access to fitness limiting resources. However, they also cooperate with group members to compete with members of other groups. In this talk I will discuss chimpanzee cooperation in the contexts of both within-and between-group competition in the Ngogo community of chimpanzees in Kibale National park. I will discuss the role of group size in cooperation, and how cooperation in the contexts of within- and between-group competition differs for males and females.

On cooperation and cognition in vervet monkeys

Redouan Bshary

Many hypothesize a tight link between our large brain and our uniquely unique cooperation skills. Experiments on primate cooperation to test this hypothesis typically take place in the laboratory. It is important to complement the resulting insights with field experiments to increase ecological validity. Vervet monkeys are highly suitable for such experiments as they live outside national parks and curious, allowing for experiments involving high quality food. I will present results on reciprocal trading and the effects of bystanders that may be replicated on other species for a comparative approach to the study of Machiavellian intelligence in non-human animals.

SUMMARY & DISCUSSION: Cooperation Session

John Mitani

FRIDAY, 31 May 2019

Competition within and between chimpanzee communities

Richard Wrangham

We often assume that conflict patterns are characteristic of a species. Yet Tai chimpanzees and Gombe chimpanzees appear to represent opposite ends of a chimpanzee continuum with respect to both intensity of intergroup violence and gregariousness of females. Are these differences stochastic? If not, are they explicable by ecological influences, or might they represent a more tolerant genotype of chimpanzees in *P. t. verus* than in *P. t. schweinfurthii*? Answers to these questions will make comparisons with other species, including non-human primates and humans, more informative concerning the relationship between within-group and between-group aggression.

Within- and between-group competition in Tai chimpanzees

Roman M. Wittig

Tai chimpanzees are possibly the least violent AND one of the most cooperative populations we know. This is surprising since competition, arising from access to resources, is supposed to be one of the main drivers for violence and cooperation. Here I will investigate the patterns of within- and between-group competition in Tai chimpanzees and relate this to the level of in-group and out-group violence and cooperation.

Within- and between group competition in Gombe and Kanyawara chimpanzees

Michael L. Wilson, Anne E. Pusey, Richard W. Wrangham

Gombe and Kanyawara provide valuable longitudinal data on competition. Gombe is hotter and drier, but at both sites, sparse food forces chimpanzees to travel in small parties during parts of the year. At both sites, intergroup interactions occur most frequently when abundant food is located in border regions. Lethal aggression occurs more frequently at Gombe, for reasons that are not fully explained. Possible factors include the high reproductive skew in Gombe's small Mitumba community, associated with intragroup killing among males, and the frequent non-dispersal of females from Gombe's Kasekela community, which provides some females with reliable allies for infanticidal attacks.

Importance of friends when competition get tough

Julia Lehmann

Having friends can be crucially important – especially in competitive environments, when having the right friend can make all the difference, sometimes even to survival. Here I am presenting data from a 'natural experiment' on Barbary macaques, assessing the importance of friends in the context of surviving a very harsh winter. More than 60% of the group members died during this winter and we found that the best predictor of survival was the availability of friends. Survivors also differed in their social network connectedness and data suggest that the availability of partners for social thermoregulation might be driving this effect.

Culture and Competition in Human Societies

Richard McElreath

Abstract: Humans societies vary in scale from family-level foragers to international empires. At every scale, individuals and groups are both in conflict and find ways to cooperate. Within families, kinship favors nepotistic cooperation, but it can simultaneously generate deadly competition for resources. In larger groups, successful competition between groups often depends upon control of competition within groups. Cultural group selection remains the only theoretically plausible account for how human societies evolved and maintain cooperation in very large unrelated groups. I'll illustrate the theory with empirical case studies, with the aim of explaining that cultural group selection is not a theory of altruism—as it is often misunderstood—but rather a theory of institutionally enforced self-interested cooperation.

SUMMARY & DISCUSSION: Competition Session

Richard Wrangham

Culture enrichment through field observations

Christophe Boesch

Animal culture studies have contributed directly to a better understanding of the complexity of this ability and in specifying the human culture uniqueness. Recent developments in the approach emphasizing the study of animal 'culture with culture' added new complementary facets to human cultural studies that were always performed 'within culture'. Improvements in the methods, in the number of populations considered and in experiments when studying wild populations have shown the great potentials over captive animal cultural studies, while at the same time bringing rigorous controls of potential confounding factors. Approaches such as field experiments with individuals living in their natural ecological and social environment, comparisons between neighboring groups living in the same environment have provided a way forward in this development. The notion of culture as a mean for individuals to adapt to new environments or complex ecological challenges seems to be supported by many of the new observations made in species like chimpanzees, capuchin monkeys, macaques as well as in birds. Future animal culture studies will help us to understand how persuasive such a notion is in the animal kingdom.

The kaleidoscope of cultural diversity in Tai chimpanzees

Lydia V. Luncz

Behavioural diversity among neighboring chimpanzee (*Pan troglodytes verus*) communities in the Tai National Park, Côte d'Ivoire has been shown to be group-specific and independent of ecological or genetic diversity. Despite frequent female transfer between groups, diversity remains stable over time with no differences between philopatric males and immigrated females, suggesting that immigrants abandoned their previous socially learned behaviour and adopt the behaviour displayed in their new group, despite previous personal knowledge that might have had fitness advantages. This level of conformity has previously only been known for humans and added valuable information to the understanding of culture in non-human animals.

Chimpanzee Material Culture in the Goulougo Triangle

Crickette Sanz & David Morgan

Wild chimpanzees provide an opportunity to identify the specific factors which have prompted the emergence and maintenance of material culture. To advance our understanding of the expression and utility of such skills in natural settings, we studied the object manipulation and tool using behaviors of chimpanzees in Republic of Congo. We examined the ecological and social contexts of these behaviors, and also compared them to sympatric gorillas in similar contexts. Environmental opportunities and social constraints played a role in the manifestation of particular types of object use, but life history traits were also influential both within and between species.

The neglected ape and its contribution to the integrative study of culture

Caroline Schuppli & Carel van Schaik

Despite being the least sociable of all great apes, our research shows that orangutans live highly cultural lives. More than two decades of data on learning, social transmission and behavioral diversity in wild populations, supplemented by data from captivity have highlighted the pervasive role of social learning in our most distant great ape relative, suggesting that human cultural capacity started to evolve at the very base of the great ape lineage. The large inter and intra population variability in social and environmental factors seen in wild orangutans has allowed us to better understand culture as function of cognition, life history, ecology and sociability.

Early human technology in the light of primate stone tool use; where do we stand?

Ignacio de la Torre

The use of stone tools by extant non-human primates is an important reference to inform the emergence and evolution of hominin technology. Chimpanzee nut cracking has been widely compared to the Oldowan and used to evaluate the technological skills of the earliest stone-tool makers. Recent research has shown wider stone tool use in other primate species than chimpanzees and humans, and provided alternative models to explain the emergence (or emergences) of lithic technology. This paper will review the empirical evidence for the origins of stone tool making, and how recent findings in the field of primatology are helping to shape our understanding of the earliest archaeological record.

SUMMARY & DISCUSSION: Culture Session

Christophe Boesch

Beyond Tinbergen's levels of analysis – Integrating mechanism and function in primate behavioral biology

Jacinta Beehner

As primate behavioral biologists, our field has traditionally focused on ultimate questions. However, as methods have become increasingly accessible, we have become more and more focused on proximate mechanisms that include: immunology, endocrinology, neurobiology, and development. These data at a proximate level of analysis can now help us understand (and update) hypotheses at an ultimate level. Not everyone agrees that integration across levels of analysis is a useful research strategy. I will use one example from geladas, male-mediated prenatal loss, to illustrate how a proximate understanding of mechanisms can, indeed, guide and refine our evolutionary hypotheses in productive ways.

The Physiology of Tai chimpanzees

Tobias Deschner

We provide an overview on the endocrinological research at Tai, spanning from female cycle patterns in relation to sexual swellings, stress and urinary glucocorticoids, energetic status and C-peptide, social bonds and oxytocin, dominance and testosterone to the measurement of immune parameters such as neopterin in relation to infections. We will put the findings in relation to publications

from other field sites as well as to measurements from other field sites performed in our laboratory. Differences and similarities in patterns across sites will be discussed with a particular focus on areas where more information is needed.

Hormones, Behavior, and Life History in Wild Chimpanzees at Kanyawara

Melissa Emery Thompson

The Kibale Chimpanzee Project has maintained an emphasis on interactions between ecology, behavior, and fitness. Hormones provide an essential layer of detail to examine how individuals respond to their physical and social environments, and in turn, what mechanisms drive variation in strategies across the life course and between individuals. Over 20 years, KCP has developed a successful physiological monitoring program addressing predictors of reproductive function, stress, and physical condition. I review how these studies have contributed to our understanding of chimpanzee socioecology and their potential to inform models for the evolution of human life history.

Insights from Genetic Analyses of the Tai Chimpanzees

Linda Vigilant, MPI-EVA, Leipzig, Germany

As one of the first groups of wild social animals subjected to detailed genetic analysis, the genetic study of the Tai chimpanzees, now in its third generation, has made important contributions on several levels. First, as a pioneering instance of the use of noninvasive sources of DNA for elucidation of individually specific genetic profiles, the results from Tai have illustrated both the potential and the pitfalls of working with challenging genetic sample materials. Second, the assessment of the distribution of paternity has elucidated the role of social rank in reproductive competition among male chimpanzees. Third, analysis of average levels of dyadic relatedness demonstrated the falsity of the long-standing assumption of high relatedness levels among males, leading to a more nuanced understanding of the impact of kinship on cooperation within as well as competition between groups. Finally, analyses of genetic differentiation among the groups at Tai has contributed to understanding the relationship between genetic and cultural variation as well as the impact of differentiation on patterns of cooperation and competition. Future insights on how the population has been shaped by selective processes such as culture, ecology, or disease will come from work on adaptive variation of immune system genes and genome-scale sequence variation.

Great Ape Health: Emerging diseases, conservation and evolutionary perspectives on human health

Fabian Leendertz

Studying health of wild great apes, our closest living relatives in the animal kingdom, allows for unraveling the interplay between sociality, health and environment, with wild great apes ultimately serving as mirrors of our deep past. In addition, data on health and disease in wild great apes may also have three important, rather applied, implications: a) the discovery of factors contributing to primate health in general, ultimately providing important information for human health, b) the identification of pathogens of importance for human health, with great apes serving as sentinels for infectious diseases and c) providing important information for conservation initiatives, resulting in targeted measures to protect wild great ape health.

SUMMARY & DISCUSSION: Physiology, Genetics, & Health Session

Jacinta Beehner

SUMMARY OF SYMPOSIUM

Carel van Schaik

END