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# Interspecies Relationships: A Zoosemiotic Analysis of Human-Ape Communication

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Department of Semiotics, Institute of Philosophy and Semiotics, University of Tartu, Estonia

The Council of the Institute of Philosophy and Semiotics of University of Tartu has, on October 25, 2021, accepted this dissertation for defense for the Degree of Doctor of Philosophy (in Semiotics and Culture Studies).

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# ACKNOWLEDGMENTS

Since I was a child, I knew that there was a path I had to take to understand the lives of other creatures. Crazy ideas would run through my mind. It was only when I came to Tartu that I realized what the path to take was. I have only just begun to scratch the surface.

I would like to give my special regards to my supervisors, Timo Maran and Nelly Mäekivi. You both have inspired and guided me ever since my MA. Your enthusiasm, passion, and professionalism have been infectious. You have shaped my mind and academic career. Nelly, I will never forget the endless calls and discussions we had, your tireless trust in my abilities and knowledge, and your everlasting motivation. Our long walks through the city and the botanical garden as well as our chats in café *Armastus* have inspired most of my ideas. Our professional relationship has blossomed into an inspiring friendship over these past few years.

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## PUBLICATIONS INCLUDED IN THE DISSERTATION

I. Cerrone, Mirko 2018. Umwelt and ape language experiments: On the role of iconicity in the human-ape pidgin language. *Biosemiotics* 11(1), 41–63.

II. Cerrone, Mirko 2019. Keepers as social companions: Tactile communication and social enrichment for captive apes. *Sign Systems Studies* 47(3/4), 453–479.

III. Cerrone, Mirko 2020. Interspecies relationships and their influence on animal handling: A case study in the Tallinn Zoological Gardens. *Biosemiotics* 13(1), 115–35.

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The contribution of the author in jointly written papers:

**Paper IV:** I was directly involved in the writing of the paper and its development. Nelly and I discussed every aspect of the paper and wrote each section four-handed. I had the main responsibility to edit the article following our reviewers' comments and for proofreading the article once it had been approved by the editor.

# INTRODUCTION

We share our spaces with a multitude of other animal species. Our fixed habitations – homes and alike – carry a strong symbolic value; they are places we recognize as safe heavens, shelters, and refuge that separate humans from other creatures. The reality is that we share our spaces with a myriad of uninvited guests, from pests such as mice to innocuous — and in fact often useful — arthropods. It is estimated that more than 579 species live in our homes (Bertone et al. 2016). If we then extend our gaze beyond domestic walls to include our yards, the number grows exponentially. The urban space is not merely human, but we cohabit it with countless animal species – including city dwellers that "move in" to exploit human resources and native species that survive alongside humans. The recognition of cities as multispecies environments is gaining momentum (Duhn 2017; Maran 2020a; Rosińska, Szydłowska 2019; Shingne 2020). Besides, we share our dwellings willingly with domesticated animals, from livestock to pets, with whom we share some of our most intimate moments and build strong emotional bonds. Considering this, interspecies communication is a topic that requires careful examination. We cannot avoid encountering other species because humans do not live in isolation from other members of the animal world. While we can hardly imagine communicating with bedbugs – who have followed humankind from their early cave dwellings (Balvín et al. 2012) – things get more complicated when we start examining our relationships with our domestic friends and with animals with more complex umwelten.

Different examples of interspecies communication can be brought up, depending on one's own definition of communication. If we consider all sign-mediated interactions as communicative events (Witzany 2006; Witzany 2008), then the discussion broadens up to include microorganisms (Federle, Bassler 2003; Ryan, Dow 2008); fungi (Antunes, Goss 2015; Cottier, Mühlschlegel 2011); plants (Stinson et al. 2006; Heil, Bueno 2007; Wolfe et al. 2008). However, here we define *communication* as the process of creation and negotiation of meaning arising from social interactions in the animal kingdom (see also paper IV). Our focus is on animals with more complex umwelten, whose social interactions are complex and multi-individual. Each species has its own perceptual and effector organs with separate phylogenetic histories that affect meaning generation in interspecific contexts. Such differences impact the selection and the processing of relevant information. The overlap of meaning in interspecies communication is much more modest when compared to intraspecies communication, which we will discuss in section IV of this dissertation.

Zoological gardens are the quintessential *hybrid environment*, as such one cannot avoid referring to the vast literature originating from such institutions[1]. Hybrid environments are places that intertwine cultural and natural elements to create complex semiotic realities. These places include other species' semiosic

[1] For a more comprehensive overview of this literature see papers II and III.

processes, apart from human-made sign systems. Interspecies relationships in hybrid environments take different shapes. Because this thesis focuses on human-ape relationships, the Tallinn Zoological Gardens has been a source of irreplaceable value for observations, interviews with keepers, and gaining first-hand experience with the work conducted in zoos, including enrichment strategies, welfare analysis, and visitor studies. The Tallinn Zoological Gardens host a multitude of primate species, including chimpanzees[2]. Besides zoological gardens, this work has also been inspired by the research conducted in centers devoted to language teaching for great apes; specifically, the work conducted by the ACCI (Ape Cognition & Conservation Initiative) with bonobos as discussed in paper I. Generally, research has favored mammals, and non-human primates are the most studied animals in zoological gardens (Stoinski et al. 1998; Rose et al. 2019). Studying human-ape relationships is one possible way to gain access to a deeper understanding of human evolution (Pereira et al. 2020), which might explain the current bias in research practice. Additionally, a closer similarity to mammalian species influences researchers' and keepers' interests (see paper III). Nevertheless, studying apes and human interactions proved to be a valuable source of knowledge when it comes to mapping the overlap of umwelten between different species. Humans and chimpanzees share 98,8% of their DNA; thus, it was also among our interests to discover how two species so phylogenetically close communicate and consolidate their relationships through social interactions.

The connecting thread throughout our publications is an expanded understanding of the concept of umwelt. Besides its application to the analysis of social communication, within our publications we have discussed the concept of "umwelt overlap" that is, the idea that the umwelt should not merely be understood as a species-specific nor as an organism-specific model, but rather it should be expanded to encompass areas of shared meanings (Lestel 1998; Lestel 2014a). These areas of shared meanings are accessible to other species due to several factors, including phylogenetic similarities and repeated, meaningful interactions (i.e., relationships). In the latter case, the concept of socialization seems to be a relevant point of discussion. The concept has been defined as "the processes by which individuals selectively acquire the skills, knowledge, attitudes, values, and motives current in the groups of which they are or will become members" (Sewell 1963). In a more semiotically oriented fashion, we could say that socialization always entails learning the code of the other individual, or the other species as we examined in our papers. This is why we propose the concept of *interspecies socialization* when studying more than one species. A more detailed terminological discussion is present in section IV of the current framework.

Different articles explore the issue from different angles. However, we may summarize the research questions behind our publications as follows:

[2] At the beginning of our research project, the Tallinn Zoological Gardens hosted three chimpanzees: one male named Pino and two females named Quincy and Betti. Unfortunately, Pino passed away in the summer of 2019.

1. How is meaning generated in interspecific communication?
2. What role does the umwelt play in meaning creation in hybrid environments?
3. How can (zoo)semiotics help to analyze interspecies communication in hybrid environments?
4. How do great apes and humans communicate in hybrid environments?
5. How is the umwelt of a species transformed during interspecies interactions?

The research questions aim to uncover how humans and apes construct meanings in hybrid environments and how species-specific sign systems are mutually changed through social interactions. We have analyzed the construction of a mutual language and the influence of species-specific characteristics in interspecific settings (cf. paper I) by highlighting the transformative power of (human) language understood as a modeling system (Sebeok 2014); we have then discussed human-ape relationships in zoological gardens and advocated for more explicit consideration of human-animal bonds for enhanced welfare (cf. paper II). In paper III, a practical study was conducted in Tallinn Zoological Gardens to investigate the relationships of keepers with the animals in their care and highlight animals' role in shaping zoo directives. All the papers included in this dissertation have utilized an Uexküllian approach; this enhances our efforts to discuss the subjective experience and communication of non-human animals by considering their species-specific traits. The umwelt model (von Uexküll 2001; von Uexküll 1992; von Uexküll 1982) has informed our discussion and helped reassess human-ape relationships by allowing us to (partially) access the phenomenological and semiotic world of other species. The concept of umwelt has not been specifically designed to analyze communication because the model was created to analyze the relation between a subject and an object. In our dissertation, we have expanded its usage and adapted it to the study of interspecific communication. By doing so, we have encountered several limitations, as highlighted in paper IV. As a matter of fact, our last publication can be understood as the culmination of our efforts: an attempt to find an appropriate approach to the description of animal communication by utilizing the Baltic-German biologist's work. We have expanded Uexküll's umwelt model (and functional circle) by combining it with the transactional model of communication created by Barnlund (Barnlund 1962; Barnlund 1970); this has allowed for the model to by applied to the analysis of social communication.

Our dissertation focuses on interspecies communication and social relations between heterospecifics; thus, most of the examples brought up in the body of this dissertation can be included in this category. Thus, in the following section, we will review a few cases of interspecies interactions that can be encountered in the animal world. The introduction will also serve as a general framework to guide readers through the argumentations and results presented in our previous publications.

# 1. INTERSPECIES RELATIONSHIPS AND COMMUNICATION

In this section, we discuss some examples of interspecies communication. This is not an easy task because the topic is quite broad and is further complicated by one's own definition of species, a concept that is not always so clear-cut (see Kull 2016 for a discussion centered on the concept of species in biosemiotics). Here we are going to focus on communication involving animal species, thus leaving aside other kingdoms.

## 1.1 Predator-prey interactions

Predators and preys engage in very complex interspecies interactions. Intraspecific codes allow animals to recognize their own species and differentiate their own from external members or competitors. Species in competition are better equipped if their code is non-transparent to their competitors; thus, from an evolutionary point of view, the absence of interspecific communication has been generally favored. For example, one can assume that predators prefer remaining unnoticed to succeed in their hunts; however, preys have evolved different ways to communicate with their predators, such as their health status or their "awareness" of predators' presence to deter attacks. This is shown in the case of rattlesnakes who warn potential predators of their dangerousness by vibrating their tails (Allf et al. 2016). A comparable phenomenon is that of *aposematism* (Poulton 1890: 339; Summers et al. 2015), which describes the presence of bright coloring evolved to warn predators of the prey's toxicity or nauseating taste, such as in the case of the granular poison frog (*Oophaga granulifera*) in the Amazon rainforest. Additionally, we can look at gazelles who will jump as high as they can when spotting an approaching cheetah. Such an unusual behavior, known as *stotting* or *pronking* (Blank 2018; Caro 1986; FitzGibbon, Fanshawe 1988), has a double meaning. Firstly, it informs the potential predator that they have been spotted; secondly, such an energy-costly behavior may only be adopted by a subject in optimal health conditions; thus, it signals that any chase would leave the predator empty-handed. This type of message is known as honest signaling (Petak 2019) because it informs the receiver truthfully about the quality of the sender (i.e., "I am healthy and strong; I will outrun you"). Humans may be either predators (often leading to mass extinction of different species) or preys, as discussed in chapter 1.5.

## 1.2 Symbiosis

Symbiosis is another interesting case of interspecies relationship. Symbiosis is a type of long-term interaction between organisms of different species that benefits both or one party. Such interactions take different forms depending on which

organism benefits from the relationship. Commensalism occurs when only one of the organisms benefits from the relationship, while the other is left unharmed; in the case of mutualistic symbiotic associations (Isack, Reyer 1989), both participants benefit from their interaction. Finally, we deal with parasitic relationships[3] when one organism (the parasite) lives on or inside the other, causing some form of harm (Wilson 1975: 354; Kull 2010b).

Symbiotic relationships do not necessarily involve communication as the two species might benefit from one another without explicitly communicating, such as in the case of clown fish (*Amphiprion ocellaris*) and sea anemones. However, symbiotic relationships often include challenges that need to be solved by one or both parties, for example, because the two species need to reach an agreement to benefit from their relationship (e.g., exchange of services) or because direct collaboration increases their chances of survival. Facing such problems often requires mutual understanding and the sharing of codes. For example, the bottom-dwelling goby (*Psilogobius mainland*) and two species of snapping shrimps (*Alpheus rapax*; *Alpheus rapacida*) have a mutualistic symbiotic relationship that is consolidated through shared communicative interactions. Gobies use burrows dug by shrimps as shelter; they sit and warn shrimps of danger by flicking their tail, while shrimps touch gobies with their antennae to communicate their presence (Preston 1978). Tactile signals exchanged by both parties benefit both the shrimps and gobies: both can escape predators more efficiently, and gobies can use burrows built by shrimps to obtain better protection against threats. Messages of this type are coded and then shared by concerned heterospecific communicators. There must exist an overlap of meaning that is consolidated through social interaction for both parties to benefit from such a relationship; this is seen in the case of the oxpecker (*Buphagus africanus*) calling out to rhinoceros or zebras before landing on their body, and zebras adjusting their posture to indicate their willingness to be cleaned (Sebeok, Ramsay 1969: 2). Another example is that of human honey-gatherers and honeyguides whose interspecies communication can be mutually beneficial (Isack, Reyer 1989).

## 1.3 Eavesdropping

Communication should be understood as an open phenomenon. Animal species may launch signals not directly addressed to specific subjects; such signals are made openly available (i.e., "to whomever it may concern") (Bouissac 2008: 3391). Thus, third parties can potentially access messages, that is, subjects who were not intended to receive the message but can exploit the information for their own good (Maran 2020b). Additionally, messages directed to specific individuals may be intercepted by third parties if the channel used by the communicators is

[3] Parasitic relationships are not always included when discussing symbiotic relationships because not all scholars agree to treat such relationships as symbiotic (see Leung, Poulin 2008 for those who include parasitism).

accessible to other species (e.g., both species rely on vocal communication in a similar range of frequencies). The decoding of such messages is possible thanks to a (partial) overlap of the perceptual and effector organs of the species. In this case, we speak of eavesdropping. It needs to be stressed that, in the case of eavesdropping, it is often unclear whether signals attended by heterospecifics are produced for communicative purposes, or rather, the third party simply interprets them based on environmental variables that are genetically transmitted (e.g., to increase chances of survival). It seems that most of the time, we are dealing with the second case; however, leaving aside the question of intentionality, we may distinguish between mutualistic eavesdropping, where both parties benefit from the exchange, and exploitive eavesdropping, where only one of the party benefits from it. Mutualistic eavesdropping can increase foraging opportunities (Morales et al. 2008) and offer better protection against predators (Anne, Rasa 1983; Baigrie et al. 2014). In the case of exploitative eavesdropping, signals will be used to take advantage of heterospecifics. This behavior is seen in some bird species who give alarm calls even when no predator is present to steal food (Flower 2011); additionally, heterospecific signals can also be exploited to improve anti-predatory strategies (Garvey et al. 2016) or to increase chances of predation (Hughes et al. 2010). Humans also exploit other animals' signals when hunting (for example, by eavesdropping on wolves' howling potential preys can be spotted).

## 1.4 Mimesis

Signals can also be employed to trick heterospecifics. This is the case for certain types of mimetic behaviors used to deceive potential predators and escape dangerous situations. Mimicry is a complex semiotic phenomenon that has already been explored elsewhere (see e.g., Maran 2003; Maran 2007; Maran 2017; Sonesson 2019). Mimicry always entails communicative aspects (Maran 2003: 205); thus, it is a topic of concern when dealing with interspecies communication. A famous example is the fork-tailed drongo (*Dicrurus adsimilis*), an African bird known to deceive heterospecifics by mimicking different alarm calls to steal food (Flower et al. 2013; Flower et al. 2014). Mimicry includes "a communicative relationship between the model and the receiver as a resemblance-based relation between the model and the mimic, and as a deceptive relation between the mimic and the receiver" (Maran 2010: 351). Vocal imitation is a widespread ability among avian species. The most classically known example is that of parrots. Parrots live in fission-fusion groups; thus, the ability to imitate vocal calls allows them to address specific individuals and distinguish outsiders from local groups (Balsby et al. 2012). Parrots living with humans learn to imitate sounds heard in domestic environments, including human speech. We can suggest that such an imitation would increase group cohesion and strengthen social bonding.

## 1.5 Different types of human-other animal interactions

Human-other-animal interactions are the focus of this dissertation. Different authors have identified the main types of relationships that man builds with other animals. For example, Thomas Sebeok addresses the types of (unusual) situations where one species' code is (partially) acquired by another species. The most common examples of human-animal interactions identified by Sebeok (Sebeok 1990: 107), which are based on Hediger's work, are classified as follows:

1. *Man as an animal exploiter* (e.g., by farming, extermination, predation, or research activities that lead to the death of the other animals or their extensive exploitation).
2. *Man as a victim of another animal* (e.g., a man killed by another animal for self-defense or feeding purposes). Sebeok liked to discuss this interaction in terms of the deadly mosquito.
3. *Man as a symbiotic (or social) partner*. This relationship may be uneven as in the case of (some) domestic animals, or of mutual dependency as in the case of guiding dogs and blind people. The relationship between keepers and captive animals highlighted in our thesis fits into this category.
4. *Parasitism*:
   a. *Man as a parasite*. This is the case of the Tungus and the reindeer who both live as nomads. The reindeer is attracted to the salt content of human urine. These populations exploit the animals' gluttony by using the tamest fawns or hinds to approach herds of wild reindeer under their disguise and then strike an attack (Zeuner 1963: 46–48). Man is effectively a social parasite.
   b. *Man as a victim of parasitism* (e.g., the above-mentioned bedbugs, flees, or ticks).
5. *Man as a conspecific*. Konrad Lorenz and his goslings is one classic example. We can also include the exceptional cases of wolf-children or keepers as social companions of apes as discussed in paper II and III.
6. *Man as a part of the environment* (e.g., insensitivity towards humans due to drastically different umwelten and/or body size). We also agree with Martinelli (Martinelli 2010: 132) that the opposite is true too: naïve observers may confuse animals with plants (e.g., corals).
7. *Humans as domesticators of other species* (and vice-versa, although not explicitly expressed by Sebeok).
8. *Humans as trainers of other animals*. Here Sebeok distinguishes between:
   a. *Apprentissage* or scientific training: experiments conducted on other species in research facilities with the aim to further scientific discoveries and knowledge.
   b. *Dressage*: training a species for the sole purpose of entertainment, such as in circuses.

Sebeok's typology has been notably elaborated on by Dario Martinelli (2010: 131–133). More specifically, he has expanded the typology proposed by Sebeok to include a few additional relationships that can be found in more contemporary settings. For example, humans can be:

9) *Manipulators of non-human animals*, from extreme cases such as genetic manipulation to aesthetics manipulations (e.g., ear-clipping).
10) *Non-human animals are a source of knowledge*.
11) *Non-human animals can be a significational source for humans*. That is, humans can turn to animals as a source of symbolic meaning (e.g., through metaphors).
12) *Humans can be protectors of other species*, as we can see with the rise of animal rights movements.

Martinelli also highlights the reciprocity of human-other-animal relationships (as already mentioned in function 5). Thus, humans can also be a source of knowledge for other animals, for example urban exploiters (e.g., pigeons) who learn human patterns for their own advantage. Similarly, humans go through changes and adaptations while domesticating other species, which we will discuss in section IV of this framework.

Particularly interesting for our thesis is the function of non-human animals as a source of knowledge for humans (and vice versa). Such a function is relevant in the context of interspecies situations because meaningful interactions between different species entail some form of knowledge acquisition, for example, through the learning of a new code. Thus, in order for any communication to happen, each species will have to partially acquire the code of the other species or construct mutually intelligible meanings through repeated interactions. Additional details on the possible working of these mechanisms will be provided in later sections; for now, we should mention that umwelt similarities facilitate interspecies communication; additionally, meaningful repeated interactions are responsible for changes in the umwelt of the subjects which we have reviewed in paper I. In paper I, ape language acquisition has been described as a special case of umwelt transition, following Morten Tønnessen's terminology (Tønnessen 2009; Tønnessen 2011).

Humans have built places where interactions between humans and other animals increase significantly, such as zoological gardens, sanctuaries, and wildlife rehabilitation centers. Because zoological gardens, sanctuaries, and wildlife rehabilitation centers host a multitude of animal species, the quantity and quality of interspecies interactions are quite complex. For example, such environments create conditions for species native from different continents to enter in contact. Thus, relationships that are usually impossible in *in-situ* environments become possible in *ex-situ* locations. Several cases of these relationships have been

reported in media: a hippo and a tortoise in Haller Park[4], the gorilla Koko and her pet kitten (Patterson 1985), and several surrogate mother programs implemented by different zoos (see for example Porton, Niebruegge 2006; Schultz et al. 2006), to name a few. Providing an exhausting, all-comprehensive analysis of the various interspecific interactions in hybrid environments would be a colossal task, besides being well beyond the scope of this dissertation. Therefore, we will instead analyze human-great-ape relationships in hybrid environments. This thesis explores human-ape interspecies relationships to uncover sign-based practices and their mutual contingency in hybrid environments. Additionally, we are interested in understanding the workings of hybrid environments to shed light on meaning creation and mutual influences within these spaces with the prospect of better animal welfare and research.

[4] Their story can be read here: https://www.npr.org/templates/story/story.php?storyId=4754996?storyId=4754996&t=1615382052536

# 2. A TRANSDISCIPLINARY APPROACH TO HUMAN-APE RELATIONSHIPS

Semiotics is at its core a transdisciplinary field. This is where the strength of a semiotic approach lies because a variety of disciplines inform semiotic investigations. Semiotics often investigates research objects from a diverse range of disciplines borrowing and building their metalanguage; thus, semiotics is open to adopting different methodologies that often overlap with the various fields they utilize. This thesis draws from multiple fields. Besides zoo biology, the main sources of inspiration for this work have been (zoo)semiotics, primatology, and philosophical discussions in human-animal studies. This dissertation includes four publications alongside the present framework, the latter concluding the discussion initiated in our research articles. We will conclude by summarizing our thoughts in addition to proposing possible future developments.

## 2.1 Zoo biology

We cannot speak of zoo biology without mentioning Heini Hediger, the founding father of the field. Hediger was concerned with a variety of topics ranging from (social) space and environmental features to improve captive animals' conditions and human-other animal interactions within zoo premises. He was openly inspired by Jakob von Uexküll, although his influence remains somewhat unexplored or underrepresented. Hediger's approach can be defined as zoocentric because it stressed the animals' perspectives as expressive subjects (Chrulew 2020), focusing on animal subjectivity. His research was based on the reconstructing the live of wildlife with close attention to the phylogenetic, individual, and group variables that need to be considered when designing enclosures. In a sense, Hediger put into practice what Uexküll had written. Hediger drew from biology scientific research to ameliorate captive animals' conditions and their captivity experience, often mitigating the transition from "the wild" to captivity (Chrulew 2018). Although his work remains irreplaceable, Hediger's heritage is almost forgotten within zoo biology (Mäekivi 2018), which has moved to treat different issues such as reproduction studies, nutrition, and other issues related to the biological needs of each species. Human-animal relations (HAR) are only a small part of the current field's research interest and can be mostly connected to a few researchers such as Hosey and Melfi (see e.g., Hosey et al. 2018; Hosey, Melfi 2014a; Hosey 2000; Hosey 2005; Hosey 2008; Hosey, Melfi 2012; Hosey, Melfi 2014b).

Nevertheless, zoo biology has proven to be a precious source of data regarding the enrichment and welfare of animals, which is especially connected to inter-species relations, as highlighted in paper II. We have provided (zoo)semiotic-inspired reflections on human-animal relationships and their impact on animal welfare in papers II and III, which suggest that human-ape (physical) interactions might be considered a source of enrichment for primates. With our work, we have

revived the original focus of zoo biology as founded by Hediger (specifically human-other-animal relationships) and connected it to contemporary work in the field and early ethological work, specifically Konrad Lorenz's work (c.f. paper II). Lorenz's early productions are characterized by a strong Uexküllian influence, explicated in his *The Companion in the Bird's World* (Lorenz 1937) before moving towards a more critical view of Uexküll's work (see Brentari 2009 for a more detailed discussion).

## 2.2 Zoosemiotics

Hediger's focus on animal subjectivity and the reconstruction of animal worlds. This effort parallels the efforts to understand non-human animals' points of view at the center of zoosemiotics, a field founded by Thomas Sebeok in 1963. Zoosemiotics can be defined as the discipline that intersects semiotics (the study of signs) and ethology, the "discipline devoted to the scientific study of signaling behavior in and across animal species" (Sebeok 1972: 61). In a broader and more contemporary sense, zoosemiotics is concerned with "the study of signification, communication and representation within and across animal species" (Maran et al. 2011: 1). Zoosemiotics, and semiotics in general, allows us to abandon an anthropocentric perspective and gain insight into other species' lives. The basic assumption of zoosemiotics is "that all animal species are social beings, each species with a characteristic set of communication problems to solve" (Sebeok, Ramsay 1969: 206). Thus, a zoosemiotic perspective enables researchers to consider animals and their umwelt, alongside their social reality. A zoosemiotic point of view favors adopting a multi-perspective approach and facilitates the analysis of complex matters by bringing out the interrelation of different phenomena that come into play in hybrid environments. A multi-perspective approach implies the use of multiple perspectives or "understandings" of the world by adopting the point of view of other species thanks to the umwelt model. Such an approach is interdisciplinary at its core.

Our dissertation has been inspired by several fields that deal with human-ape interactions, and more generally, studies concerned with human-other-animal interactions. It is important to consider the impact of Hediger's work on Thomas Sebeok's writings. Sebeok himself considered Hediger an important figure within biosemiotics (Sebeok 2001b; Sebeok 2001a). As mentioned earlier, Hediger's categorization of human-animal relationships (Hediger 1964) was echoed in Sebeok's work (Sebeok 1972; Sebeok 1990), who expanded and elaborated it by bringing out the already semiotically oriented approach of Hediger. Sebeok's treatment of interspecies communication is more explicit when compared to that of Hediger, who instead focused on "relations" (Hediger 1964) and "expressions" (Hediger 1970). Sebeok defines interspecies communication as entailing "more than one specific code, the number depending on the complexity of the ecosystem occupied by animals belonging to different species that congregate there to their mutual advantage" (Sebeok, Umiker-Sebeok 1980: 2).

Following Martinelli's path, zoosemiotics' mission should be to 1) investigate whether properties conceived as uniquely human can be found in other animal species; and 2) to study the role of other animals in human life and, more broadly, culture – the latter goal belonging to the area of anthropological zoosemiotics. Our research tries to find a balance between the two goals: on the one hand, we have investigated whether properties conceived as uniquely human (e.g., belonging to language) could find equivalent counterparts within the animal kingdom. On the other hand, we explored the role played by non-human-animals in human society by specifically looking at human-ape relationships within zoological gardens. Our goal was to look at human-ape relationships as a gateway to understand the mutual influences within hybrid environments. We also uncovered the role of animal agency within zoological gardens by highlighting the impact of animal actions on institutional regulations (c.f. paper III). In our dissertation, we are mostly concerned with the second mission highlighted by Marinelli; that is, we have highlighted humans' role as (social) partners of apes; however, special mention should be paid to the fifth type of relationship in Sebeok's typology, *Man as a conspecific*. We have emphasized that keepers might be considered as an extended member of the social group in paper II; in paper III, we have brought up the idea that keepers themselves perceive their relationship with the chimpanzees in their care as especially meaningful, to the extent that many of the keepers reported the importance of being "part of their group". Finally, in paper II, we have accentuated how hybrid environments create the condition for the creation of shared meanings resulting from repeated interactions, common interests, and affections. While we would not go as far as to claim that captive animals see keepers (or researchers) as conspecifics (at least in those cases we have analyzed), there is certainly an overlap that is worth investigating.

## 2.3 Primatology

The importance of being accepted within a group is an essential prerequisite to the research conducted by primatologists, such as Jane Goodall (2010), Shirley Strum, and Dian Fossey (2000). It is also a core principle of Japanese primatology. In this dissertation we have used several ideas stemming from primatology, specifically ideas concerning the social structures in primate societies to exemplify the types of possible relationships that apes can build with their human partners.

Japanese primatology uses a "participant observation" methodology, which is quite different from the commonly adopted methodologies of Western schools (Matsuzawa 2017). Western schools instead favor a more objectively distant approach. In the participant observation method, a triadic relationship is established between the researcher, infant, and mother. Japanese primatologists seek to establish strong, trustworthy bonds with the chimpanzees they are studying, allowing mothers to trust researchers to handle their infants. The research paradigm of Japanese primatology emphasizes the subjective character of relationships, besides stressing the importance of individual-level differences of each

subjective chimpanzee. Unlike most of the contemporary Western approaches, Japanese primatology does not shy away from subjectivism. The field's core principles can be summarized by the term *kyōkan*, a term coined by the Japanese primatologist Masao Kawai (1969). The term can be roughly translated as "feel-one", and Kawai used it to describe a characteristic of Japanese primatology: understanding other primates from an empathetic perspective rather than in an objective way (Langlitz 2020: 41). Such methodology allows researchers to make use of anthropomorphic descriptions to increase empathetic understanding of the studied primates (Asquith 1981; Burghardt 1985). However, it needs to be stressed that while the methodologies employed in Western primatology strive towards objectivism, the seminal work of the Trimates[5] shows a different angle. They used individual descriptions within their work, building a strong empathetic bond with the apes they were studying. Their work is filled with descriptions of individual traits of their apes, who were given names and recognized unique personalities. The field of ethology has classically shown a more significant interest in describing species and group behavior, leaving aside the focus on individuals. However, research with primates since the 1950s has shifted the paradigm in unorthodox ways. As scientific rigor did not allow for individual and obscured individuality (Birke 1994: 7), the work of the Trimates also includes autobiographical works in which the lives of the authors are narrated together with those of other animals. As a matter of fact, these authors live(d) among the animals they described and, to an extent, have created authentic hybrid communities with them. The process of habituation necessary to observe wild animals without disturbing them has clear parallels with techniques familiar to ethnographic research (Shah 2018: 132). In ethnographic work, researchers need to integrate themselves within the observed community to participate in social life.

Similarly, primatologists are accepted by the primates under study as "non-threatening", and they can become, to an extent, social partners (Fossey 2000: 172) and elicit intraspecific behavior. Becoming "part of the group" also means that part of the social attention is directed towards researchers, and besides the dangers of aggression, human presence can influence animal behavior to an unknown extent. However, when speaking about primatological research, we must mention that within semi-participatory methods researchers are rather accepted outsiders within the group and do not engage fully in communal and social life. Hobaiter et al. have questioned the extent to which human researcher influence the animal groups under study (Hobaiter et al. 2017). Nevertheless, we should avoid the pitfall of considering human influence negatively as if "wild" animals have ceased to exist and have been corrupted by human interference. In our work, we have rather accentuated what Hediger defined as a "catalytic effect" (Hediger 1981), namely behavioral transformations that are the result of repeated human-animal relationships. This idea can be connected to the concept of "umwelt overlap" which we

[5] Jane Goodall, Dian Fossey, and Birutė Galdikas are often referred to by the term trimates as they were originally chosen by the anthropologist Louis Leakey to study chimpanzees, gorillas, and orangutans, respectively.

have developed in our publications (paper III, paper IV) and will explore deeper in the following sections. The catalytic effect is stronger when umwelt similarities are more accentuated. It is also worth considering that human-other-animal interactions potentially increase empathy which can improve mutual understanding. Humans also act as a recorder of other species' individual histories:

> Some animals have an authentic history – a shared social memory – as primatologists have demonstrated in chimpanzees. Such history influences behaviour, preferences, and representations in animal societies all the more since a human serves as an animal's active memory by acting as if the animal had historical memory. The animal has access to its history in two ways – through its own memory (as seen in chimpanzees, for example), which rather remains an autobiographical memory that is shared in part, and through borrowed memory, in this instance, the human's memory, which serves as an external trace of the animal's actions. (Lestel 2014b: 122)

One should not underestimate the fact that other animals, as active agents, create their own history, shape their environment, and impact other subjects they interact with. Human-other-animal communities always entail mutualistic aspects that need to be thoroughly considered; thus, in our work, we have tried to bring out those aspects and highlighted the role other animals have on human's semiotic systems, including cultural products (cf., paper III).

In the work of early primatologists, apes are treated as subjects, and their lives are portrayed with a style that acquires a quasi-ethnological taste (Shah 2018: 120). The use of ethnographic methods to study human-other-animal relationships has been advocated by Arluke and Sanders (1996) and applied to different extents empirically (see e.g. Alger, Alger 1999; Jaroš 2018). One of the advantages of such a methodology is that it allows for an analysis of data from a sociologically informed perspective; it enables researchers to consider the intersubjectivity in a multispecies environment with a participatory approach to research. A similar approach can be indeed found in zoosemiotic research. Zoosemiotics research investigates "animal meanings through comparative, participatory and context-sensitive (reciprocal) approaches" (Maran et al. 2016: 23). A more detailed discussion on this dissertation's methodological approach can be found in the next section.

# 3. METHODOLOGICAL CONSIDERATIONS

A unanimous definition of semiotics is hard to find; in this thesis, we understand it as the study of signs and sign processes that lead to meaning creation. As mentioned in chapter 2, the systemic investigation of semiosis in the animal kingdom, including non-verbal sign relations in humans, is a topic of concern for zoosemiotics. Human-other-animal relationships have been investigated in various fields, including philosophy, anthropology, medicine, biology, to name a few. Zoosemiotic research often uses data stemming from other fields, for example, from ethology or zoo biology. Quantitative studies and statistics used in these fields offer a solid basis for discussion; however, zoosemiotics usually uses qualitative research as it provides a more flexible and open methodology that is best suited for the study of other animal species. One of the advantages of quantitative studies is that it allows researchers to gather generalizable data on a macro-level. In animal studies, quantitative methods may provide a list of behaviors and their frequency (e.g., in ethograms) by answering *what*-questions. Qualitative research, instead, answers *why*-questions and *how*-questions by offering a degree of flexibility that quantitative studies lack, besides allowing researchers to focus on "marginal" or specific cases. Mixed methods may combine positive aspects of both methodologies and allow for deeper explorations. For example, mixed methods are informed by generalizable data and interpretative strategies but mitigate the disadvantages of both methods (such as the far too strict reliance on numbers in the case of quantitative research and the small sample sizes and possible overgeneralizations of qualitative studies).

## 3.1 Untangling a zoosemiotic approach

The field of zoosemiotics can be divided into different branches, each with a specific focus. Sebeok distinguished between pure, descriptive, and applied zoosemiotics (Sebeok 1972: 87). Pure zoosemiotics is concerned with the elaboration of theoretical models; descriptive zoosemiotics with the description of signaling and communicative behavior of animals; while applied zoosemiotics strives to apply the knowledge and data gathered for human benefits. Martinelli proposed a more complex classification by distinguishing between *Ethological Zoosemiotics* and *Anthropological Zoosemiotics* (Martinelli 2010: 9–10). One can further divide ethological zoosemiotics between an early period, mostly concerned with the development of a paradigm for a new arising discipline and a specific focus on communication issues (inspired by Lorenz and behaviorists), and a modern approach devoted to the discussion of animal semiosis in general, embracing cognitive approaches inspired by Griffin's work.

Anthropological zoosemiotics instead refers to the study of the interactions of humans and other animals, anticipated by the work of Sebeok and Heini Hediger. One should speak of *communicational anthropological zoosemiotics* when con-

sidering communication issues between humans and other animal species. When one of the communicators is human, the adoption of an emic perspective is facilitated because we mostly share a common understanding, and at the very least, we can use language to gain insights into other people's world. Adopting an emic position with other species is a more arduous task due to biological differences and the lack of a common language. However, the umwelt model offers a valuable solution as it allows researchers to gain partial access to the perceptive and effector worlds of other organisms. *Significational/representational anthropological zoosemiotics* is the sub-branch of zoosemiotics concerned with other animals as a source of meaning, an object of semiosis rather than a subject (Martinelli 2010: 10). In this case, scholars are not only concerned with the study of myths, tales, allegories, and other stories but also scientific works, such as taxonomy or guidelines for animal handling.

This thesis takes a middle ground. In our publications, we balance pure, descriptive, and applied strategies to offer a renewed understanding of semiotic phenomena in hybrid environments (paper I, paper II, paper III) and propose a possible application to better both interspecies relationships and the welfare of captive animals (paper II, paper III). Finally, our last publication (paper IV) can be read as the culmination of our efforts to design a zoosemiotic model that could be sufficiently employed in the study of social communication. On the one hand, we are inspired by the Uexküllian tradition and early ethological work of Lorenz (early Ethological Zoosemiotics) and reconcile it with the current focus on semiosis and cognitive issues, mainly informed by zoo biology and primatology. On the other hand, our work is mainly oriented towards Anthropological Zoosemiotics. Our research interest lies in studying human-ape relationships with an evident focus on the communicative issues that characterize communicative anthropological zoosemiotics. While we have not focused specifically on the central issues of significational/representational zoosemiotics, a few reflections on the significational role of animals are present (for example, within zoo guidelines in paper II; human understanding of other animals in paper III).

In paper I, close reading was employed to offer a semiotically oriented reinterpretation of the ape language experiments. Previous research was mostly focused on the mere passive reproduction of signs and syntactic combinations rather than on the way apes creatively use language; this has led to the creations of diverse methodologies conceived to teach human language to apes that are based on extremely rigid criteria that do not treat apes as creative subjects. An umwelt-oriented analysis has allowed us to overcome such problems by highlighting species-specific features and their influence in experimental settings and bring forward semiotic properties of ape language. The umwelt model also offered an emic perspective into the world of another species without falling too deeply into the trap of anthropomorphism.

Paper II deals with a topic that overlaps with zoo biology and ethology. We highlighted tactile communication, a species-specific communication channel that is often overlooked within communication studies. Previous research has overemphasized the role of visual-auditorial channels or rather underrepresented

other channels in other species due to a verbocentric understanding of communication. Our research linked zoo biology work to early and modern ethological research and offered a synthetic interpretation of touch as a species-specific communication device that should be utilized to enhance captive conditions of primates. We have explored and analyzed keeper-ape relationships from such a perspective using the lens of umwelt theory. Keepers are recognized as social partners of the animals in their care; thus, the paper explores ape-human relationships and treats humans as a form of social enrichment that potentially may enhance animal welfare.

In paper III we have used qualitative research strategies to investigate keeper-animal relationships in the Tallinn Zoological Gardens. Interviews were conducted with three keepers who worked with chimpanzees (*Pan troglodytes*), saltwater crocodiles (*Crocodylus porosus*), and pygmy marmosets (*Cebuella pygmae*). Our study took a bi-constructivist approach (Lestel et al. 2014), where we treated keepers' experiences and anecdotal stories as primary sources of information. In our study, we decided to opt for a qualitative approach because such an approach offers insights into the personal experience of keepers, besides allowing a more direct focus on specific, local issues. Data were analyzed through an *ad hoc* approach that merged deductive and inductive reasoning. Qualitative research allowed us to explore social interactions within zoos and provided an in-depth understanding of the ways keepers understand, act upon, and manage their daily interactions with the animals in their care. Finally, a qualitative study also allows the contextualization of previous data gathered through quantitative studies, specifically stemming from zoo biology and ethology. Our study highlighted the way human perception of animals influences one's relationship with them and, in turn, how different understanding of animal agency impacts work handling, enrichments strategies, and, potentially, animal welfare.

Finally, paper IV can be read as a synthetic presentation of our results and includes concluding remarks and possible solutions to one of the core questions of the thesis: how to study social communication from an emic perspective through the lens of umwelt theory. As a matter of fact, while we have resorted to the work of Uexküll in order to tackle the various issues presented in our paper, we have encountered a few obstacles along the way. The model was not conceived to address communication specifically, although it has since been adapted to be used in such a context (see paper IV). Moreover, previous applications of the umwelt model tended to overemphasize species-specific realities, neglecting individual-level variety and areas of shared meanings existing across species, as we will discuss in the following section. We have designed a transactional model of animal communication by combining Barlund's transactional communication model (Barnlund 1962; Barnlund 1970) and the umwelt model. Our elaborated model offers a valuable solution to the analysis of intraspecies communication that is aware of the role of private and public cues, subjects' specific behaviors, messages, and the context in creating meaning. The model also shows great potential in the study of interspecies communication as it enables researchers to consider the

species-specific and potentially overlapping nature of meanings created in social interactions.

In the next section, we will deal with the study of social communication through the lens of the umwelt theory by highlighting the advantages and disadvantages offered by the model. Finally, we will discuss our proposal in more detail and illustrate how our transactional model of animal communication offers a solution to the limitations found in previous communication models and in the umwelt model.

# 4. COMMUNICATION IN HYBRID ENVIRONMENTS

Relations between humans and other animals vary in quantity and kind. In our second article we have discussed the types of relationships that other animals might have with humans; these relationships can be positive, neutral, or negative (Hosey, Melfi 2014a; Hosey 2008; Hosey, Melfi 2012; Hosey, Melfi 2014b). Ultimately, human-other-animal relationships are influenced by different variables, including the familiarity of animals and humans and species-specific features.

Hediger classifies human-other-animals' relationships into two major groups (Hediger 1964: 154), as represented in the following scheme (Figure 1.).

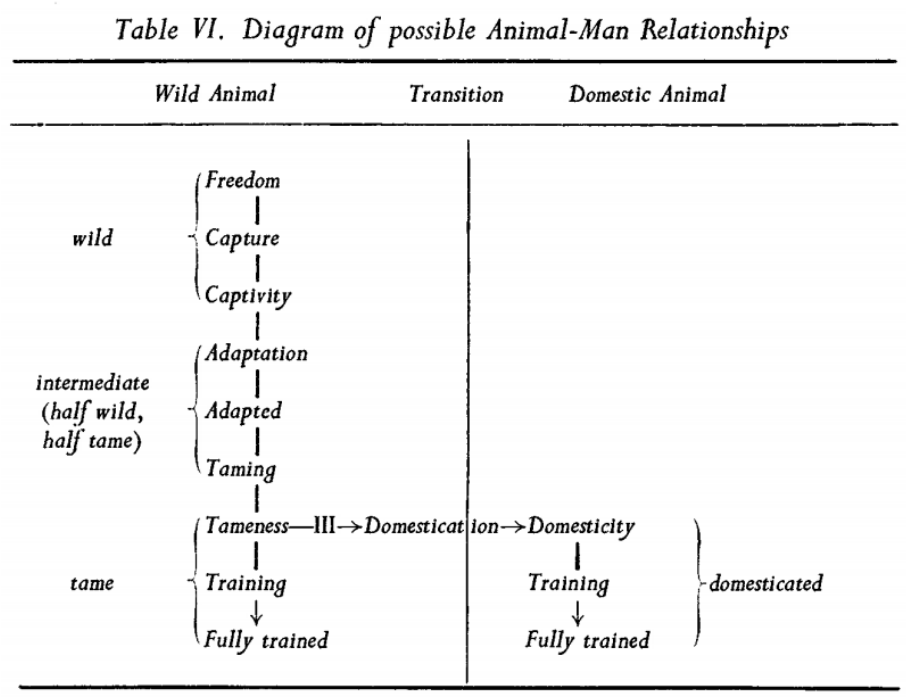


**Figure 1.** Various degrees of relationships. From Hediger 1964, 154.

His classification is based on how much human contact a specific animal species experience. He, therefore, speaks of wild and domestic animals, acknowledging that there might be nuances that escape such a dichotomic classification.

Hediger's classification demonstrates the different stages through which animal species go through as their familiarity with humans increases. However, it is important to make a distinction between the concept of tameness and that of domestication. While various definitions exist and the two phenomena largely overlap, we can define tameness as the (gradual) process that reduces flight distance. An animal may be tamed through a process of habituation, that is "the

loss of an animal's fear response to people arising from frequent non-consequential encounters" (McNay 2002: 833). Permanent genetic changes may lead to an innate predisposition towards humans; hence, we can speak of domestication. For Hediger, tamed zoo animals are not domesticated because genetic changes are not transmitted through different generations; however, the domesticated status of captive animals is not always clear-cut[6]. For example, it has been argued that human presence interferes with the hunting habit of chimpanzees (Hobaiter et al. 2017). As a matter of fact, it is often necessary for researchers to be accepted as non-threatening (neutral role) or as part of the social group in order to observe animal behavior. Some animal species have been observed in the wild for decades; thus, it is unclear whether genetic changes have been initiated by human inference through scientific observations and then transmitted through generations.

We would go as far as to argue that many domesticated species are not behaviorally tame, at least not in the traditional sense. Dairy cows are commonly much more docile when compared to beef cattle. For example, Agnus cows show higher resistance to human contact and more aggressive behavior than their dairy relatives. In zoological gardens taming acquires a tremendous significance. Captive animals need to be tamed because humans handle them daily. Reducing their flight distance means a facilitated and safer job for their keeper and a less stressful experience for the nonhuman-animals.

The proposed definition of domestication, however, remains one-sided. It overestimates the controlling role of humans and underrepresents the active role of other animals in shaping their relationships with humans. In a zoosemiotic sense, domestication affects both sides. Domestication might be understood as a mutualistic, interspecific communication process involving a "domesticated" and a "domesticating" species as active agents (Kleisner, Stella 2009: 456). This is why the authors have proposed the concept of co-domestication to represent such a two-sided phenomenon better. According to this perspective, man has undergone a domestication process, adapting to an ever-changing environment. Meanings are created and changed during the process by both species, resulting in a greater integration of one species with the other than before the process started. According to Kleisner and Stella, domestication *in sensu lato* includes animals that are not typically considered domestic (e.g., lab rodents and zoo animals would fall in this category). The authors understand domestication as a "process of genetic and ontogenetic adaptation of an organism to the conditions of culture" (Kleisner, Stella 2009: 459).

A concept linked to domestication is that of socialization. In the field of zoo biology, the concept has been employed to describe "the process, where animals

[6] It is important to note that the status of animals in captivity has been questioned because humans exert control over other animals held in zoos to a great extent. The Species360 program lets zoos share information about their animals. This database allows different institutions to decide which animals to exchange to guarantee genetic diversity through mating. Contrary to Hediger's beliefs, zoo animals genetic code is constantly being controlled by humans.

routinely interact with people and become familiar with them, leading to changes in the human-animal relationship" (Hosey et al. 2013: 232). A relationship is formed by repeated interaction between two (or more) individuals leading to increased predictability about the outcome of future interactions (Hosey et al. 2013: 483). The strongest relationships, formed on the basis of repeated, positive interactions, lead to the formation of bonds. Bonds are characterized by individual relationships formed by non-human animals and humans, they are reciprocal and persistent, and they ultimately tend to improve the wellbeing of both parties (Russow 2002).

In this thesis we define socialization as "the processes by which individuals selectively acquire the skills, knowledge, attitudes, values, and motives current in the groups of which they are or will become members" (Sewell 1963). Unlike domestication, socialization entails a different set of behavioral and cognitive changes that are not necessarily genetically transmitted; it also differs from taming as socialization requires the adoption of attitudes and values and not a mere reduction of flight distance. All domestic and tamed animals are, to an extent, socialized. However, the level of socialization varies according to the species. Such variability depends on different factors, including species-specific characteristics, human interest (e.g., what type of relationship an animal has with humans), and individual predispositions. Thus, dogs are more heavily socialized than livestock because dogs are kept as pets and often treated as family members, while livestock is raised to produce labor or commodities such as meat, eggs, milk, fur, and leather. Species-specific characteristics influence the success of domestication and socialization. For example, it is estimated that dogs were domesticated from wolves about 16,000-17,000 years ago (Morey, Jeger 2015). It is suggested that excess meat among human societies, wolves' (*Canis lupus*) social nature, and their ability to adapt to rapid environmental changes are among the reasons why this species was successfully domesticated. Conversely, cheetahs' domestication has failed because these animals struggle to mate in captive environments (Kor Oldenbroek 2007: 77). Lastly, individual-level dispositions affect animals' integration within human communities, as individual animals might be more prone to show affiliative behavior towards humans than others.

## 4.1 Interspecies socialization

We may speak of *interspecies socialization* when learning involves different species. To the best of our knowledge, the concept was first introduced by social anthropologist and primatologist Gabriela Bezerra De Malo Daly (2019) to describe the process through which one species learns the behavior of another through social interactions or when a species learns one's own species-specific behavior thanks to the aid of another species (Daly 2019: 93). However, referring back to our working definition of socialization, we speak of interspecies socialization when a species may learn the behavior, skills, knowledge, attitudes, values, and motives of another species. Learning may occur through interactions

motivated by unusual circumstances (e.g., captive conditions); however, such a phenomenon is frequent in *in-situ* environments as well (Musser et al. 2014), most significantly when shared living space enhancing chances of survival (Schmitt et al. 2016).

Interspecies socialization is facilitated by similarity in umwelten, similar perceptual and effector organs, and any pre-existing overlaps of meanings in the two species' repertoire. We might go as far as to say that most animal species are capable of interspecies socialization. The extent varies according to the species natural propensity to social life; however, similarities in umwelten allow the two species to acquire knowledge about the other species more efficiently. In our case, we are concerned with human-ape socialization and interspecies relationships. The International Primatological Society (IPS) establishes that "Human interaction, even where it is welcomed by the animal, should never be seen as a substitute for conspecifics and does not meet the social needs of a non-human primate" (2007: 11). However, we disagree with such a statement because it tends to simplify very complex and multileveled relationships without considering that positive human interactions can indeed be beneficial for captive animals. If we acknowledge that human-animal interactions are inevitable in captive environments, then improving relationships should be one of the goals of zoological gardens. Channeling positive relationships can improve the welfare of captive animals (Cerrone 2019). Enculturated apes are apes raised in mixed human environments and exposed to human culture and language; they are among the clearest products of interspecies socialization. However, the term "enculturated" fails to capture the nuance of the situation. The term stresses apes' acquisition of human behavioral and cultural patterns while downplaying humans' acquisition of apes' communicative strategies and behavior. A neglected aspect within such a framework is the influence of non-human animals on humans' sign systems and communication, specifically in the context highlighted here. While it is true that enculturated apes are exposed to human cultural products to a greater extent, it needs to be stressed that researchers (humans) are equally creators and users of hybrid cultural practices. Humans may also learn from apes' species-specific repertoire. For example, keepers often use pan-hoot and grunts to communicate with the apes in their care (Daly 2018); grooming may also be used as a tool for social bonding (see paper II) with positive effects for both apes and humans alike.

In this case, interspecies socialization has a deep-rooted effect upon the communication, and cognitive systems of the animals as a new (human-made) sign system has been taught and implemented into the daily lives of apes. We have referred in our publications to such instances as examples of "hybrid communities", by referring to the work of French philosopher Dominique Lestel (Lestel 1998; Lestel 2014a). Such communities are funded upon shared interests, affects, and meanings that link two or more species. The language used by great apes is modeled after apes' cognitive and physical abilities, besides being influenced by species-specific structures, as we have argued in paper I. In this sense, ape-human pidgin results from an interspecies interaction, a two-way system developed through social exchanges to accommodate the needs of two different species.

Ape-human communities have agreed to use a sign system that is suitable and adaptable to both species' physical and cognitive needs; nevertheless, research paradigms have underestimated such phenomenon and only focused on how human-like was the use of language by apes, as argued in our first article.

## 4.2 Umwelt overlap

The concept of umwelt has been mostly employed on a species-specific level, although Uexküll mostly dealt with individual animals in his analyses. A brief search in literature reveals the tendency to understand the model as a species-specific subjective world (Deely 2001; Kull 2010a: 47). Such an interpretation is grounded in the work of Uexküll. Uexküll compared umwelten to invisible bubbles filled with perceptions that only its inhabitant (a subject) can access (von Uexküll 1992: 319). Indeed, the umwelt model has been accused of exacerbating a subjectivist understanding of reality and promoting excessive separateness between subjects. As we have argued in our publications, these aspects have been overemphasized in literature, ignoring that shared representations and mutual interactions also exist. We stress the importance of understanding umwelten as overlapping realities.

In Uexküll's work, ecological relations appear in the form of a duet. Relationships between organisms are explained through music analogies: the properties of a subject (point) find their counterpoint in the properties of another subject. One example is that of the spider and the fly (von Uexküll 2001: 122). The spider weaves its web, which is invisible to the fly. The threads of its web are strong enough to trap the insect, and the mash of the web relates well to the body size of the fly. The spider, however, weaves its web before it even encounters its first fly. For Uexküll, who was not enthusiastic about Darwinian theories, harmony reigns over the design of nature. There is a tiny window that opens in the umwelt of a spider that allows the predator to lean out the world of the fly. Such a window facilitates the survival of one species because it enables the predator to exploit some features of its prey for its own advantage. However, Uexküll is mostly concerned with the design of the body and contrapuntal relationships existing between pairs, as in the case of tree leaves and rain droplets or the female-male duet that allows mating and reproduction. The overlap between umwelten that we have described in our articles extends beyond such cases to embrace communicative and broader cognitive features.

Overlaps are rooted in physiological features (i.e., body plan including perceptual and effector organs) but they extend beyond these. Existing overlaps can be strengthened, and new overlapping areas can be created with repeated, meaningful interactions. Similar phylogenetic histories allow species to share genetic and communicative codes, as in the case of many big cat species (e.g., lions and tigers). Similarities in body structures facilitate interactions and communication (cf., paper II), and allows species to build stronger relationships based on shared meanings and interests. Additionally, we proposed that repeated interactions can

increase the already existing overlaps between two (or more) individuals. This is the case with domestication and increased understanding between species coexisting in the same space (Jaroš 2016; Jaroš 2018), as highlighted earlier.

Umwelt similarities facilitate interspecies socialization and communication. In our fourth article, we have designed a communication model that considers the umwelt of the species; we designed a zoosemiotic approach to the transactional communication model inspired by Barnlund (Barnlund 1962; Barnlund 1970). Such a model has been conceived to facilitate the study of animal communication (including humans) by keeping in mind the species-specific and umwelt-specific features of each communicator. While we have designed our model to tackle intraspecific communication specifically, the model can be extended to include the analysis of interspecies communication. As a matter of fact, one of the advantages of our model lies in its ability to represent the individual and species-specific character of meaning generated during the communicative process. Besides, umwelten can also be expanded to include elements of other species' umwelten (or mutual languages can be created *ex-novo*) through socialization. Different animal species may consolidate their relationships through repeated interactions, generate shared meanings, and create mutually intelligible languages. In zoological gardens, apes are not language-trained[7]. However, these animals are still socialized and often share interests, meanings, and strong emotional bonds with their keepers. We argued that keepers might be seen as social companions. Thus, they provide the necessary social interactions and contribute to improving welfare by providing additional enrichment opportunities. Our field research at Tallinn Zoological Gardens uncovered how keeper-ape relationships affect daily practices within zoological gardens. Specifically, close relationships allow keepers to monitor individual animals and satisfy their requests more efficiently. Keepers grant greater agency to these animals because they can discern individual needs, which may translate into better welfare. On the other side, the extent to which umwelt differences and human attitudes impact animal welfare in captivity should be questioned. In paper III, we have directly addressed reptilian welfare and enrichment strategies and discovered that lack of strong bonds between animals and keepers affects the types of enrichment strategies used for these animals, which in turn may influence their welfare negatively.

[7] Apes in zoological gardens are nevertheless exposed to language and, reportedly, understand several words, phrases, and commands used by their keepers.

# CONCLUSIONS

These few chapters provide an exhaustive framework for the publications included in this dissertation and give some conclusive remarks to the work carried out over the past four years. Interspecies communication is a complex semiotic topic that requires careful examination. However, the topic has not received the attention it deserves. As humans, we tend to project human-like properties on other animals, thus assuming other species' point of view has been a difficult challenge to overcome; this thesis is one attempt to create a path for mutual understanding. Additionally, humans tend to take on a subsuming role over other species, thus perpetuating the idea that humanity sits on top of the *scala naturae* and other species are nothing more than imperfect versions of humans.

This thesis used a zoosemiotic perspective to answer our research questions and shed light on how interspecies relationships orchestrate meaning generation in hybrid environments. Much of our work owes its finding to the theories of Jakob von Uexküll. The umwelt model proved to be an irreplaceable tool for inquiring into the lives of other species as it enabled us to reconstruct the semiotic world of other creatures without falling too deeply into the trap of anthropomorphism. However, we faced some adversities and limitations when applying the model to the analysis of interspecies communication because of how the model had been originally conceived, as brought up in section 3 and paper IV.

The most relevant findings of our work can be summarized as follows:

- Language, understood as a modeling system, shapes the communicative and other cognitive faculties of non-human animals (cf. paper I). While language allows for richer interactions between humans and non-humans, language also modifies intraspecific relations as demonstrated in language-competent apes (e.g., Washoe tried teaching sign language to her offspring, and bonobos at the ACCI use linguistic tokens to make requests).
    - Mutually intelligible languages are created that allow two different species to communicate. Different animal species go through an extensive process of modification of their semiotic environment due to the acquisition and usage of new signs (cf., paper I), a phenomenon that we have linked to the concept of umwelt transition (Tønnessen 2009; Tønnessen 2011).

- Animals with more complex umwelten must have cognitive and social needs met when kept in captive conditions, besides having their physical needs attended. Keepers and scientists can form strong emotional bonds with the animals in their care. Keepers of apes can be social companions of apes in captivity (cf. paper II).
    - The catalyst effect of keepers may elicit intraspecific behavior and enrich apes' living conditions by providing multilayered social interactions. Additionally, keeper-ape interactions create new meanings and shared sign systems that can potentially reach outside individual relationships and influence internal, intraspecific group dynamics (cf. paper II and III).

- Animals in captivity shape institutional practices and other human-made sign systems. Some animals may bring changes to institutional practices by influencing handling practices, including enrichment and work routines (cf. paper III). These animals have partial control over their captive lives that can impact institutional regulations (e.g., type of contact and regulated activities), besides actively shaping their interactions with keepers. For example, chimpanzees at the Tallinn Zoological Gardens exert choices that modify handling practices and "tweak" zoo routines with a deeper-lasting effect upon the zoo's practices and regulations.
    - Repeated interactions bring about new meanings and behaviors within hybrid environments (cf. paper I, III, III). Positive keeper-ape relationships should be encouraged and built to better the welfare of captive animals and workers alike.

- The umwelt model has proven to be an inspiring and powerful tool which we have used to (partially) access the world of other organisms and take their point of view. Nevertheless, we have faced some difficulties when approaching social communication, as illustrated in paper IV and the previous section of this dissertation.
    - Our expanded vision of the umwelt model depicts communication as a semiosic process. Meaning is the result of a negotiation process dependent on the species-specific and individual peculiarities of the communication parties. Umwelten of social species should be studied in relation to other organisms. This is particularly important when trying to study communication by taking an Uexküllian approach.

- The overlap between different umwelten is much less extensive than in the case of intraspecies communication. Interspecies communication is characterized by a decreased number of public cues (Cpu-s) and an increased number of private cues (Cpr-s). The level of overlap between the umwelten of the communicators will influence the amount of meaningful behavioral cues (Cbeh-s). The interpretation of behavioral cues depends on the compatibility of the species communication repertoire, which ultimately is dependent on the perceptual and effectual organs of the communicators. Finally, our model can be used to analyze interspecies communication where one of the subjects is an other-than-human animal, and the other is human. This proves to be especially important in the ever-expanding hybrid environments where human lives are connected with those of other animals' lives (zoological gardens and laboratories, as in our case studies).

To conclude, we would like to leave a few reflections on future directions and imagine the next steps needed to dig deeper into the topic of interspecies relationships. We have focused on ape-human relationships, further attempts to understand how umwelt similarities could be utilized to access the world of other

animals to better their conditions in captivity. This work has focused on species that are closely related to humans; however, it paved the way to approaching the study of other species in a similar manner. Our communication model can be adapted to the study of creatures that are less similar to human beings, as it takes into account each species' umwelten and communication channels. Future research should bring attention to other species, especially those that more often than not are uninteresting to mainstream research and media (e.g., reptiles).

Abandoning an anthropocentric point of view will be one of the challenges to solve, as social, communicative, and physiological needs vary according to species. A careful examination of human attitudes, umwelt analyses, and an empirical application of our expanded communication model might serve as a basis upon which future discussions can be developed. Theoretical studies allow broader generalizations that enable researchers to design future studies and overcome foreseeable challenges. A theoretical framework was necessary for the development of a communication model that was flexible enough to be adopted and adapted in different scenarios. However, we recognize the importance of empirical research as a necessary step to further research. We strive to utilize our model to improve animal welfare in captivity; hence, our approach should not only be appreciated in a heuristic manner. The understanding of umwelt as malleable, overlapping realities will be one of the key factors to utilize when reaching into interspecies relationships. In the age of Anthropocene, human influence is stronger than ever; however, other animal species should not be understood as passive recipients but as active subjects capable of shaping their own reality and relationships with the organisms they interact with. We hope that we have paved the way for further studies focusing on animal agency and its role in interspecific relationships, including communication issues.

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# SUMMARY IN ESTONIAN

## Liikide vahelised suhted: inimeste ja inimahvide vahelise kommunikatsiooni zoosemiootiline analüüs

Antud lõputöö keskendub inimeste ja inimahvide vahelistele suhetele ja kommunikatsioonile hübriidsetes keskkondades, mida määratleme keeruliste semiootiliste reaalsustena, milles põimuvad kultuurilised ja looduslikud elemendid. Olenevalt kommunikatsiooni definitsioonist võib tuua erinevaid näiteid liikide vahelise kommunikatsiooni kohta. Meie määratleme *kommunikatsiooni* kui sotsiaalse lävimise protsessi, mille käigus loomariigis tähendust luuakse. Meie tähelepanu on koondunud kompleksete omailmadega loomadele, kelle sotsiaalne kommunikatsioon on keeruline ja hõlmab sageli paljusid indiviide.

Lõputöösse kaasatud artiklite ühendav teema on laiendatud arusaam omailma mõistest. Lisaks omailma rakendamisele sotsiaalse kommunikatsiooni analüüsile oleme oma artiklites käsitlenud „omailma kattuvuse“ mõistet, st ideed, et omailma ei tuleks mõista ainult liigi- ega organismispetsiifilise mudelina, vaid pigem tuleks seda laiendada, et see hõlmaks jagatud tähendusi. Need jagatud tähendused on teistele liikidele kättesaadavad mitmete tegurite, sealhulgas fülogeneetiliste sarnasuste ja korduvate tähenduslike koostoimimiste (st suhete) tõttu.

See väitekiri sisaldab praeguse raamistiku kõrval nelja publikatsiooni, millest viimane lõpetab meie teadusartiklites algatatud arutelu. Erinevad artiklid uurivad läbivat teemat erinevatest vaatepunktidest. Siiski võime oma artiklite uurimisküsimused kokku võtta järgmiselt:

1. *Kuidas tekib tähendus liikide vahelises kommunikatsioonis?*
2. *Millist rolli mängib omailm tähenduste loomisel hübriidsetes keskkondades?*
3. *Kuidas saab (zoo)semiootika aidata analüüsida liikide vahelist kommunikatsiooni hübriidsetes keskkondades?*
4. *Kuidas kommunikeeruvad inimahvid ja inimesed hübriidsetes keskkondades?*
5. *Kuidas muutub liigi omailm liikide vahelise kommunikatsiooni käigus?*

Eesmärk on uurida, kuidas inimesed ja inimahvid konstrueerivad tähendusi hübriidsetes keskkondades ja kuidas liigispetsiifilisi märgisüsteeme sotsiaalsete interaktsioonide kaudu vastastikku muudetakse.

Esimeses artiklis kasutame lähilugemist, et pakkuda inimahvide keele omandamise katsetele semiootilist tõlgendust. Omailmale suunatud analüüs võimaldab meil sellistest probleemidest üle saada, tuues esile liigispetsiifilised tunnused ja nende mõju katsetingimustes ning tuues esile ahvide keele semiootilised omadused. Omailma mudel pakub ka eemilise perspektiivi teise liigi maailma, ilma liiga sügavale antropomorfismi lõksu langemiseta.

Teine artikkel käsitleb teemat, mis kattub loomaaia bioloogia ja etoloogiaga. Tõstame esile taktiilse kommunikatsiooni kui liigispetsiifilise kommunikatsioonikanali, mis kommunikatsiooniuuringutes sageli tähelepanuta jääb. Meie

uurimus seob loomaaia bioloogia uurimissuuna etoloogiaga ning pakub tõlgenuse puudutusest kui liigispetsiifilisest kommunikatsioonist, mida tuleks rakendada primaatide tehistingimuste parandamiseks. Uurime ja analüüsime ulukihooldajate ja inimahvide vahelisi suhteid lähtuvalt omailma teooriast. Ulukihooldajaid nähakse nende hoole all olevate loomade sotsiaalsete partneritena; seega uurib artikkel inimahvide ja inimeste suhteid ning käsitleb inimesi kui sotsiaalse rikastamise vormi, mis võib suurendada loomade heaolu.

Kolmandas artiklis kasutame kvalitatiivseid uurimismeetodeid, et analüüsida ulukohooldajate ja loomade suhteid Tallinna Loomaaias. Intervjuud tehti kolme ulukihooldajaga, kes töötavad koos šimpansitega (*Pan* troglodytes), krokodillidega (*Crocodylus porosus*) ja kääbusmarmosettidega (*Cebuella pygmae*). Meie uuring toob esile, et viis, kuidas inimene looma tajub, mõjutab suhteid loomaga. Lisaks näitame, kuidas erinev arusaam loomade agentsusest mõjutab tööd loomadega, rikastamisstrateegiaid ja potentsiaalselt ka loomade heaolu.

Neljandat artiklit võib lugeda meie tulemuste sünteesiks ning see sisaldab kokkuvõtvaid märkusi ja võimalikke lahendusi ühele lõputöö põhiküsimusele: kuidas uurida sotsiaalset kommunikatsiooni eemilisest vaatenurgast läbi omailma teooria. Kuigi oleme kasutanud Uexkülli töid, et vastata meie artiklis esitatud küsimustele, oleme kokku puutunud mõningate takistustega. Omailma mudel ei ole kavandatud konkreetselt kommunikatsiooni käsitlemiseks, kuigi seda on kohandatud sellises kontekstis kasutamiseks. Meie väljatöötatud mudel pakub liikide vahelise kommunikatsiooni analüüsile väärtuslikku lahendust, mis arvestab privaatsete ja avalike viidete, subjektidele iseäraliku käitumise, sõnumite ja konteksti rolli tähenduse loomisel.

Lõputöö esimeses osas käsitleme mõningaid liikide vahelise kommunikatsiooni näiteid. Teises osas toome välja oma lähenemisviisi erinevad teabeallikad. Arutame loomaaia bioloogia, primatoloogia ja zoosemiootika mõju meie tööle, tuues välja semiootiliste tööde transdistsiplinaarse olemuse. Kolmandas osas käsitleme oma töö metodoloogilist tausta. Semiootika tegeleb sageli erinevate distsipliinide uurimisobjektidega, laenates ja ehitades nende metakeelt. Seega on semiootika avatud erinevatele metoodikatele, mis sageli kattuvad laenatud uurimisobjekti distsipliiniga. Neljandas osas käsitleme liikide vahelise sotsialiseerimise ja omailma kattuvuse mõistet, mille oleme oma artiklites välja töötanud. Oma väitekirjas oleme laiendanud omailma mudeli kasutamist ja kohandanud seda liikide vahelise kommunikatsiooni uurimiseks.

Töö viimane osa esitab meie uurimisprojekti peamised tulemused, mille võib kokku võtta järgmiselt:

- Keel, mida mõistetakse modelleerimissüsteemina, kujundab loomade kommunikatiivseid ja muid kognitiivseid võimeid (vt I artikkel). Kuigi keel võimaldab inimeste ja teiste loomade vahel rikkalikumat lävimist, muudab see ka liigisiseseid suhteid, nagu on näidatud keelepädevate ahvide puhul (nt Washoe proovis oma järglastele viipekeelt õpetada ja bonobodele on soovide väljendamiseks õpetatud kasutama leksigramme).

- Luuakse vastastikku arusaadavad keeled, mis võimaldavad kahel erineval liigil kommunikeerida. Erinevad loomaliigid läbivad oma semiootilise keskkonna ulatusliku muutmise protsessi, kuna omandavad ja kasutavad uusi märke. Oleme seda nähtust seostanud omailma ülemineku mõistega.

- Komplekssemate omailmadega loomadel peavad tehistingimustes lisaks nende füüsilistele vajadustele olema täidetud kognitiivsed ja sotsiaalsed vajadused. Ulukihooldajad ja teadlased võivad hoolealuste loomadega luua tugevaid emotsionaalseid sidemeid. Inimahvide hooldajad võivad olla tehistingimustes loomadele sotsiaalsed kaaslased.
  - Ulukihooldajate mõju võib nende hoolealustel esile kutsuda liigisisese käitumise mitmekesistumist ja rikastada inimahvide elutingimusi, pakkudes mitmekihilist sotsiaalset lävimist. Lisaks loovad ulukohooldaja ja inimahvide interaktsioonid uusi tähendusi ja jagatud märgisüsteeme, mis võivad potentsiaalselt jõuda väljapoole individuaalseid suhteid ja mõjutada liigisisest rühmadünaamikat.

- Tehistingimustes peetavad loomad mõjutavad institutsionaalseid praktikaid ja muid inimese loodud märgisüsteeme. Näiteks võivad mõned loomad mõjutada hooldamispraktikaid, sealhulgas rikastamist ja tööprotsesse. Nendel loomadel on osaline kontroll oma tehistingimustes elatava elu üle ja see võib mõjutada institutsionaalseid eeskirju (nt kontakti tüüp ja reguleeritud tegevus) ning lisaks aktiivselt kujundada nende lävimist ulukihooldajatega. Näiteks teevad Tallinna Loomaaia šimpansid valikuid, mis muudavad hooldamispraktikaid ja „kohandavad“ loomaaia rutiini, avaldades sügavamat mõju loomaaia praktikatele ja eeskirjadele.
  - Korduvad interaktsioonid toovad hübriidsetes keskkondades kaasa uusi tähendusi ja käitumist. Ulukihooldajate ja inimahvide positiivseid suhteid tuleks julgustada, et parandada nii tehistingimustes peetavate loomade kui ka töötajate heaolu.

- Omailma mudel on osutunud inspireerivaks ja võimsaks vahendiks, mida oleme kasutanud teiste loomade maailmadele (osaliselt) juurdepääsemiseks ja eemilise perspektiivi saavutamiseks. Sellele vaatamata oleme sotsiaalsele kommunikatsioonile lähenedes silmitsi seisnud mõningate raskustega, nagu on näidatud IV artiklis ja antud väitekirja eelmises osas.
  - Meie laiendatud nägemus omailma mudelist kujutab kommunikatsiooni kui semioosilist protsessi. Tähendus on läbirääkimisprotsessi tulemus, mis sõltub kommunikatsioonipartnerite liigispetsiifilistest ja individuaalsetest iseärasustest. Sotsiaalsete liikide omailmasid tuleks uurida seoses teiste organismidega. See on eriti oluline, kui kommunikatsiooni uuritakse Uexkülli lähenemise abil.

- Erinevate omailmade kattumine on liikide vahelises kommunikatsioonis palju vähem ulatuslik kui liigisisese kommunikatsiooni puhul. Liikide vahelist

kommunikatsiooni iseloomustab avalike viidete (Cpu) vähenemine ja privaatsete viidete (Cpr) suurenemine. Kommunikatsioonipartnerite omailmade vahelise kattumise tase mõjutab tähenduslike käitumisviidete (Cbeh) hulka. Käitumisviidete tõlgendamine sõltub liikide märgirepertuaaride ühilduvusest, mis sõltub omakorda kommunikeerijate taju- ja mõjuelunditest.

Meie mudelit saab rakendada liikide vahelise kommunikatsiooni analüüsimiseks, kus üheks osapooleks on inimene ja teiseks mõni muu loom. See osutub eriti oluliseks üha laienevates hübriidsetes keskkondades, kus inimeste elud on tihedalt seotud teiste loomade eludega (nt loomaaiad ja laborid, nagu ka meie juhtumiuuringute kese).

# PUBLICATIONS

# CURRICULUM VITAE


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| 2019–2020 | University of Tartu, (FLSE.00.260) Zoosemiotics: Umwelt and Animal Communication (seminars) |
| 2020–2021 | University of Tartu, (FLSE.00.251) Readings of J. v. Uexküll and J. Lotman |
| 21.10.2019 – …. | Tartu Waldorf School, Teacher (0,65) |

**Acknowledgements**

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|---|---|
| 2018 | Biosemiotics Achievement Award |

**Education**

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|---|---|
| 29.08.2016 – | University of Tartu, studies in semiotics and cultural studies. PhD thesis "*Enculturated Apes: Loss of Iconicity and the Role of the Body in the Ape Language Experiments*". |
| 2014–2016 | University of Tartu, studies in semiotics and cultural studies. MA thesis (*cum laude*), "*A Semiotic Analysis of the Research Paradigms Behind the Ape Language Experiments*". |
| 03.09.2012 – 30.06.2013 | University of Tartu, Department of Philosophy, Visiting student |
| 09.2010 – 03.2014 | University of Salerno, Foreign Languages and Literature, Russian and English. BA thesis (*cum laude*) *"L'italiano popolare: da un corpus di semicolti salernitani"* (People's Italian: a written collection by semiliterate Salternitan writers" |
| 2005–2010 | Istituto Magistrale "Teresa Confalonieri", secondary education. |

**Publications**

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| 6.3 | 2020 | Harrik, Airika; Cerrone, Mirko (2020). Šimpans võib mõjutada loomaaia töökorraldust soojade suhetega. *Novaator* |
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| 5.2 | 2018 | Cerrone, Mirko (2018). Tactile Communication in Captive Apes: Keeper–Animal Interspecies Communication. *Semiotics of Hybrid Natures: Anthropogenic ecosystems, multimodalities, transformed umwelts, University of Tartu, Estonia, 8–10 November.* Ed. Silver Rattasepp. University of Tartu, 24−25. |

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| 6.7 | 2016 | Mirko Cerrone (2016). *A Semiotic Analysis of the Research Paradigms Behind the Ape Language Experiments*. (Magistritöö, Tartu University). University of Tartu. |

# ELULOOKIRJELDUS

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| 2019–2020 | University of Tartu, (FLSE.00.260) Zoosemiotics: Umwelt and Animal Communication (seminars) |
| 2020–2021 | University of Tartu, (FLSE.00.251) Readings of J. v. Uexküll and J. Lotman |
| 21.10.2019 – … | Tartu Waldorf School, Teacher (0,65) |

**Tunnustused**

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| 2018 | Biosemiotics Achievement Award |

**Haridus**

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**Publikatsioonid**

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