Measuring communicative complexity across modalities: a new framework in the context of the “social complexity hypothesis” and its application in true lemurs

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Summary

Animals exhibit an astonishing diversity of communicative systems, with substantial variation in both the nature and the number of signals they produce. Variation in communicative complexity has been conceptually and empirically attributed to social complexity and formalized as the “social-complexity hypothesis for communicative complexity” (SCHCC). Indeed, group-living animals face complex social environments where they engage in a wide range of interactions with different social partners triggering the need for transmission of a broader diversity of messages.

In **chapter I** (Peckre et al. 2019), I review the literature on the current tests of the SCHCC, pointing out and discussing what I identified as the main gaps in the current state of the art. Specifically, three key issues emerged from my analysis. The first issue concerns the operational definition of the main variables, social and communicative complexity. Notably, when defining communicative complexity, most empirical tests of the SCHCC focus on a single modality (e.g., acoustic, visual, olfactory) whereas several good reasons exist for acknowledging the multimodal nature of both, signals and communicative systems in this framework. At the system level, focusing on only one modality may lead to over- or underestimation of the relationship between social and communicative complexity. The second issue relates to the fact that while numerous studies have highlighted a link between social and communicative complexity, their correlative nature does not permit conclusions about the direction of causality. Indeed, alternative hypotheses involving anatomical, phylogenetical, or ecological factors have also been proposed to explain the evolution of more complex forms of communication. Finally, I note that researchers rarely address the actual ways in which social factors directly affect variation in signaling. Indeed, the underlying mechanisms of this link are usually left unexplored, failing to uncover the specific attribute of communication that would be co-evolving with specific aspects of sociality. I, therefore, make a plea for expanding tests of the SCHCC in 1) scope (systematic approach across modalities) and 2) depth (characterization of the observed relationships) as I believe it may significantly advance our understanding of the intricate links between animal sociality and communication.

To address point 1), I offer in **chapter II** a comprehensive approach of the cross-modal communicative systems of two closely related true lemur species having similar morphology, living in similar habitats, but differing in their social systems. I studied wild *Eulemur rufifrons* and *E. mongoz* in Madagascar, respectively in Kirindy and Ankatsabe forests for 12 months. I describe a new analytical framework to assess the complexity of signaling systems across modalities. Applying a multimodal approach may help to uncover the different selective pressures acting on the communicative system and to understand better adaptive functions that might be unclear from the study of its separate components

independently. *E. rufifrons,* the species having the more complex social system, also had overall a more complex communicative system than the one of the *E. mongoz.* Both careful choices of the species to compare to limit the effect of possible additional selective pressures and exploration of the social function of the non-homologous signals allow concluding that this increased complexity of the communicative system in E. rufifrons is most likely associated with social selective pressures. I developed this new analytical framework, partly based on using a cross-modal network approach, with the perspective of facilitating cross-taxonomic comparisons. Moreover, this approach may be combined with new multi-dimensional approaches of social complexity and contribute to a more holistic approach to the tests of the SCHCC. By this, we should be able to derive new testable hypotheses that would contribute to better understand the course of events that have led to the evolution of communication diversity in its distinct dimensions.

In **chapter III**, I address point 2) by investigating the impacts of sociality on the expression of a multimodal signal, the anogenital scent-marking behavior in wild red-fronted lemurs. I specifically investigated intragroup audience effects on anogenital scent-marking behaviors in a wild population of red-fronted lemurs and particularly whether males and females differed in this aspect and if these differences may reveal functional differences associated with anogenital scent-marking across sexes. I found an intragroup audience effect in males but not in females. Males deposited less often anogenital marks when more males were present within a three meters range compared to five- or ten-meters ranges. Males may prefer to reduce the risk of physical contact by avoiding to scent-mark near other males, and/or give priority to other males to scent-mark. With these results, I provide important insights into the functional significance of anogenital scent-marking in red-fronted lemurs and support the idea of greater intragroup social pressures associated with anogenital scent-marking in males than in females in egalitarian species. Studying the flexibility of complex signal usage (e.g., occurrence or structural modifications) across social contexts (audiences) should permit the identification of different individual social characteristics that may elicit or constrain complex signal expression. These social characteristics may later constitute social pressures acting for or against the evolution of these complex signaling behaviors.

In **chapters IV** and **V,** I also address ethical questions related to this project and the way I tried to adapt and best address my responsibilities for animal welfare. In chapter IV, I expose some technical details and ethical concerns experienced during the choice of my field sites. While in chapter V (Buil and Peckre et al. 2019) I present a remote releasable collar system developed in collaboration with the Neurobiology Laboratory (German Primate Center, Göttingen, Germany) intending to provide a tool to significantly reduce the number of captures in studies using bio-logging for medium-sized mammal species.

Overall, by emphasizing the importance of the multimodal nature of communicative systems and the social context in which signals are exchanged, I hope to stimulate the development of new tests of the SCHCC based on this expanded framework. I additionally argue for the importance of looking across research fields since striking parallels may be observed between animal behavior and linguistic research when addressing the origins of communication complexity, be it in the form of human language or animal signaling.

Zusammenfassung

Die Studie der kommunikativen Komplexität über verschiedene Modalitäten: Ein neuer Ansatz im Kontext der „Sozialen Komplexitätshypothese“ und seine Anwendung in der Gattung Eulemur.

Tiere verfügen über eine erstaunliche Vielfalt an Kommunikationssystemen, die sich in ihrer Beschaffenheit und in der Anzahl an produzierten Signalen wesentlich unterscheiden. Diese Varianz in der kommunikativen Komplexität wurde konzeptionell und empirisch der sozialen Komplexität zugeschrieben und als “social-complexity hypothesis for communicative complexity” (SCHCC) zusammengefasst. So sind gruppenlebende Tiere mit einem komplexen sozialen Umfeld konfrontiert, in dem sie in einer Vielzahl an Interaktionen mit Sozialpartnern agieren und somit auch eine größere Vielfalt an Signalen überbringen müssen.

In Kapitel I (Peckre et al. 2019) rezensiere ich die Literatur über die derzeitigen Tests der SKHKK und diskutiere die größten Lücken, die ich in der bisherigen Forschung identifiziert habe. Drei zentrale Aspekte kamen dabei zum Vorschein. Der erste Aspekt betrifft die Arbeitsdefinition der Hauptvariablen soziale und kommunikative Komplexität. Die meisten empirischen Tests der SKHKK fokussieren sich auf eine einzige Modalität (z.B. akustisch, visuell, olfaktorisch), wenn sie kommunikative Komplexität definieren, doch es gibt viele wichtige Gründe die multimodale Beschaffenheit der Signale und der Kommunikationssysteme zu berücksichtigen. Auf der Ebene der Kommunikationssysteme kann das Fokussieren auf nur eine Modalität dazu führen, dass der Zusammenhang zwischen sozialer und kommunikativer Komplexität über- oder unterschätzt wird. Der zweite Aspekt bezieht sich auf die Tatsache, dass zahlreiche Studien einen Zusammenhang zwischen sozialer und kommunikativer Komplexität hervorheben, sich jedoch bei diesen Korrelationen keine Rückschlüsse auf Kausalitäten machen lassen. Tatsächlich wurden auch alternative Hypothesen herangezogen, die anatomische, phylogenetische und ökologische Faktoren berücksichtigen, um die Evolution komplexerer Kommunikation zu erklären. Zum Schluss weise ich darauf hin, dass Wissenschaftler selten die tatsächliche Art und Weise identifizieren, durch die soziale Faktoren Unterschiede in Signalen direkt beeinflussen. Da diese Mechanismen meist unerforscht bleiben, bleiben auch die spezifischen Eigenschaften der Kommunikation unentdeckt, die sich in der Evolution zusammen mit den unterschiedlichen Aspekten der Sozialität entwickelt haben. Daher plädiere ich dafür, dass die Tests der SKHKK 1) in ihrem Umfang (systematischer Ansatz über verschiedene Modalitäten) und 2) in ihrer Tiefe (Charakterisierung der beobachteten

Zusammenhänge) erweitert werden. Dies wird bedeutend dazu beitragen, die komplexen Zusammenhänge zwischen der Sozialität von Tieren und ihrer Kommunikation zu verstehen.

Um Punkt 1) zu adressieren, widme ich mich in Kapitel II in einem ganzheitlichen Ansatz den crossmodalen Kommunikationssystemen zweier nahverwandter *Eulemur* Arten, die über gleiche Morphologie und ähnlichen Habitate, aber unterschiedliche Sozialsysteme verfügen. Hierfür habe ich für 12 Monate wildlebende *E. rufifrons* (in Kirindy) und *E. mongoz* (in Ankatsabe) in Madagaskar studiert. Um diesen Vergleich der zwei verschiedenen Arten zu erleichtern, habe ich einen neuen Analyserahmen entwickelt, der die Komplexität der Signalsysteme verschiedener Modalitäten erfasst. Dieser multimodale Ansatz kann helfen, unterschiedliche Selektionsdrucke, die auf das Kommunikationssystem wirken, zu erkennen und adaptive Funktionen besser zu verstehen, welche bei separaten Untersuchungen der einzelnen Komponenten der Kommunikation unklar bleiben. *E. rufifrons*, die Art mit dem komplexeren sozialen System, hatte auch insgesamt ein komplexeres kommunikatives System als das von E. mongoz. Sowohl die sorgfältige Auswahl der zu vergleichenden Arten, um die Auswirkungen möglicher zusätzlicher Selektionsdrücke zu begrenzen, als auch die Erforschung der sozialen Funktion der nicht-homologen Signale lassen den Schluss zu, dass diese erhöhte Komplexität des kommunikativen Systems bei E. rufifrons höchstwahrscheinlich mit sozialen Selektionsdrücken verbunden ist. Ich habe diesen neuen analytischen Rahmen entwickelt, der zum Teil auf der Verwendung eines cross-modalen Netzwerkansatzes basiert, mit der Perspektive, taxonomische Vergleiche zu erleichtern. Schlussendlich kann dieser neue Ansatz in Kombination mit der mehrdimensionalen Berücksichtigung der sozialen Komplexität eine ganzheitlichere Bewertung der SKHKK ermöglichen. Auf diese Weise sollten wir in der Lage sein, neue testbare Hypothesen abzuleiten, die dazu beitragen würden, den Ablauf der Ereignisse besser zu verstehen, die zur Evolution der Kommunikationsvielfalt in ihren verschiedenen Dimensionen geführt haben.

In Kapitel III widme ich mich Punkt 2), indem ich den Einfluss von Sozialität auf das Benutzen eines multimodalen Signals, dem Setzen von anogenitalen Duftmarken beim Rotstirnmaki (*Eulemur rufifrons*) untersuche. Ich untersuche insbesondere den Effekt des sozialen Kontexts, d.h. den Effekt der Empfänger/ Zuschauer auf das Verwenden von Duftmarken in einer wilden Population von Rotstirnlemuren und insbesondere, ob sich Männchen und Weibchen in diesem Aspekt unterscheiden und ob diese Unterschiede funktionelle Unterschiede im Zusammenhang mit der anogenitalen Duftmarkierung zwischen den Geschlechtern aufzeigen können. Ich fand einen gruppeninternen Publikumseffekt bei Männchen, aber nicht bei Weibchen. Männchen legten weniger häufig Anogenitalmarkierungen ab, wenn mehr Männchen in einem Umkreis von drei Metern anwesend waren, verglichen mit einem Umkreis von fünf oder zehn Metern. Möglicherweise ziehen es die Männchen vor, das Risiko eines Körperkontakts zu verringern, indem sie die Duftmarkierung in der Nähe anderer Männchen vermeiden und/oder anderen Männchen den Vorrang bei der Duftmarkierung geben. Mit diesen Ergebnissen liefere ich wichtige Einblicke in die funktionelle Bedeutung der anogenitalen Duftmarkierung bei Rotstirnlemuren und unterstütze die Idee eines größeren sozialen Drucks innerhalb der Gruppe, der mit der anogenitalen Duftmarkierung bei Männchen verbunden ist, als bei Weibchen in egalitären Arten. Indem wir erforschen, wie flexibel komplexe Signale benutzt werden (z.B. ob es Flexibilität oder strukturelle Modifizierungen gibt) in den unterschiedlichen sozialen Kontexten (Empfängern), können wir unterschiedliche individuelle soziale Charakteristika besser identifizieren, die das Nutzen komplexer Signale begünstigen oder einschränken. Diese sozialen Charakteristika können dann soziale Selektionsfaktoren darstellen, die die Evolution von komplexem Signalverhalten beeinflussen.

Des Weiteren, beziehe ich mich in Kapitel IV und V auch auf die ethischen Fragen bezüglich der Forschung für meine Doktorarbeit und erkläre wie ich der Verantwortung für das Wohlergehen der Tiere nachgehe. In Kapitel IV lege ich einige technische Details und ethische Bedenken dar, die ich bei der Auswahl meiner Feldstandorte erfahren habe. In Kapitel V (Buil and Peckre et al. 2019) stelle ich ein ferngesteuertes, abnehmbares Halsbandsystem vor, das in Zusammenarbeit mit dem Labor für Neurobiologie (Deutsches Primatenzentrum, Göttingen, Deutschland) entwickelt wurde, um ein Werkzeug zur Verfügung zu stellen, mit dem die Anzahl der Fänge in Studien mit Bio-Logging für mittelgroße Säugetierarten deutlich reduziert werden kann.

Mit meiner Arbeit möchte ich dazu beitragen, dass in zukünftigen Studien neue, erweiterte Testansätze für die SKHKK entwickelt werden, indem ich die Bedeutung der multimodalen Art und Weise der Kommunikationssysteme und die Wichtigkeit des sozialen Kontexts, in dem Signale ausgetauscht werden, hervorhebe. Des Weiteren wird es wichtig sein, Forschungsbereiche zu erweitern, da sich, wenn es um den Ursprung der kommunikativen Komplexität geht, markante Parallelen zwischen den Wissenschaftsfeldern Verhaltens-forschung bei Tieren und der Linguistik aufdecken lassen. Sei es in Form der menschlichen Sprache oder der kommunikativen Signale im Tierreich.

Résumé

Mesurer la complexité communicationnelle à travers les modalités : un nouveau cadre dans le contexte de l'"hypothèse de la complexité sociale" et son application chez les lémuriens.

Les animaux présentent une étonnante diversité de systèmes de communication, avec des variations substantielles tant dans la nature que dans le nombre de signaux qu'ils produisent. La variation de la complexité communicationnelle a été conceptuellement et empiriquement attribuée à la complexité sociale et formulée comme "l'hypothèse de la complexité sociale" (SCHCC pour “Social-Complexity Hypothesis for Communicative Complexity”). En effet, les animaux vivant en groupe sont confrontés à des environnements sociaux complexes où ils s'engagent dans un large éventail d'interactions avec différents partenaires sociaux, ce qui rend nécessaire la transmission d'une plus grande diversité de messages.

Dans le chapitre I (Peckre et al. 2019), je passe en revue la littérature sur les tests actuels de la SCHCC, en soulignant et en discutant ce que j'ai identifié comme les principales lacunes dans l'état de l'art. Plus précisément, trois questions clés sont ressorties de mon analyse. La première question concerne la définition opérationnelle des variables principales, complexité sociale et communicationnelle. Notamment, pour définir la complexité communicative, la plupart des tests empiriques de la SCHCC se concentrent sur une seule modalité (par exemple, acoustique, visuelle, olfactive) alors qu'il existe plusieurs bonnes raisons de reconnaître la nature multimodale des signaux et des systèmes communicatifs dans ce cadre. Au niveau du système, se concentrer sur une seule modalité peut conduire à une sur- ou sous-estimation de la relation entre la complexité sociale et communicative. La deuxième question concerne le fait que, si de nombreuses études ont mis en évidence un lien entre la complexité sociale et communicative, leur nature corrélative ne permet pas de conclure sur la direction de cette causalité. En effet, des hypothèses alternatives impliquant des facteurs anatomiques, phylogénétiques ou écologiques ont également été proposées pour expliquer l'évolution de formes de communication plus complexes. Enfin, je note que les chercheurs se penchent rarement sur la nature réelle des liens par lesquels les facteurs sociaux affectent directement la variation de l’expression des signaux. En effet, les mécanismes sous-jacents à ces liens sont généralement laissés inexplorés, ne permettant pas de mettre en lumière l'attribut spécifique de la communication qui évoluerait conjointement avec des aspects spécifiques de la socialité. Je plaide donc en faveur d'une extension des tests de la SCHCC en termes 1) d'étendue (approche systématique à travers les différentes modalités de

communication) et 2) de profondeur (caractérisation des relations observées), car je pense que cela pourrait faire progresser de manière significative notre compréhension des liens complexes entre socialité et communication animales.

Pour aborder le point 1), je propose dans le chapitre II une approche globale des systèmes de communication intermodale de deux espèces cousines de lémuriens, ayant une morphologie similaire, vivant dans des habitats similaires, mais différant dans leurs systèmes sociaux. J'ai étudié des *Eulemur rufifrons* et des *E. mongoz* en liberté à Madagascar, respectivement dans les forêts de Kirindy et d'Ankatsabe pendant 12 mois. Je décris un nouveau cadre analytique pour évaluer la complexité des systèmes de signalisation à travers les différentes modalités de communication. L'application d'une approche multimodale peut aider à mettre en lumière les différentes pressions sélectives agissant sur le système de communication et à mieux comprendre les fonctions adaptatives qui pourraient être invisibles par l'étude indépendante de ses composants séparés. E. rufifrons, l'espèce ayant le système social le plus complexe, avait également un système de communication globalement plus complexe que celui d'E. mongoz. Le choix minutieux des espèces à comparer pour limiter l'effet d'éventuelles pressions sélectives supplémentaires et l'exploration de la fonction sociale des signaux non-homologues permettent de conclure que cette complexité accrue du système de communication chez E. rufifrons est très probablement associée à des pressions sélectives sociales. J'ai développé ce nouveau cadre analytique, en partie basé sur l'utilisation d'une approche de réseau inter-modalités, dans l'optique de faciliter les comparaisons inter-taxonomiques. De plus, cette approche peut être combinée avec de nouvelles approches multidimensionnelles de la complexité sociale et contribuer à une approche plus holistique des tests de la SCHCC. Ainsi, nous devrions être en mesure de dériver de nouvelles hypothèses testables qui contribueraient à mieux comprendre le cours des événements qui ont conduit à l'évolution de la diversité de la communication dans ses différentes dimensions.

Dans le chapitre III, j'aborde le point 2) en étudiant les impacts de la socialité sur l'expression d'un signal multimodal, le comportement de marquage olfactif anogénital chez les lémuriens à front roux. J'ai spécifiquement étudié les effets de l'audience intragroupe sur les comportements de marquage olfactif anogénital dans une population de lémuriens à front roux en liberté, en particulier si les mâles et les femelles diffèrent dans cet aspect et si ces différences peuvent révéler des différences fonctionnelles associées au marquage olfactif anogénital entre les sexes. J'ai trouvé un effet d'audience intragroupe chez les mâles mais pas chez les femelles. Les mâles déposaient moins souvent des marques anogénitales lorsque qu'un plus grand nombre de mâles étaient présents dans un rayon de trois mètres (mais pas de cinq ou dix mètres). Les mâles pourraient préférer réduire le risque de contact physique en évitant de marquer près d'autres mâles, et/ou donner la priorité aux autres mâles pour marquer. Avec ces résultats, je fournis des informations importantes sur la signification fonctionnelle du marquage olfactif anogénital chez les lémuriens à front roux et je soutiens l'idée de pressions sociales intragroupe plus importantes associées au marquage olfactif anogénital chez les mâles que chez les femelles chez les espèces égalitaires. L'étude de la flexibilité de l'utilisation des signaux complexes (par exemple, l'occurrence ou les modifications structurelles) en fonction des contextes sociaux (audiences) devrait permettre d'identifier les différentes caractéristiques sociales individuelles qui peuvent susciter ou limiter l'expression de signaux complexes. Ces caractéristiques peuvent ensuite constituer des pressions sociales agissant pour ou contre l'évolution de ces comportements de signalisation complexes.

Dans les chapitres IV et V, j'aborde également les questions éthiques liées à ce projet et la manière dont j'ai essayé de m'adapter et d'assumer au mieux mes responsabilités en matière de bien-être animal. Dans le chapitre IV, j'expose certains détails techniques et les problèmes éthiques rencontrés lors du choix de mes sites de terrain. Dans le chapitre V (Buil and Peckre et al. 2019), je présente un système de collier détachable à distance développé en collaboration avec le Laboratoire de neurobiologie (Centre allemand des primates, Göttingen, Allemagne) dans le but de fournir un outil permettant de réduire de manière significative le nombre de captures dans les études utilisant le bio-logging pour les espèces de mammifères de taille moyenne.

Globalement, en soulignant l'importance de la nature multimodale des systèmes de communication et du contexte social dans lequel les signaux sont échangés, j'espère stimuler le développement de nouveaux tests de la SCHCC basés sur ce cadre élargi. En outre, j'insiste sur l'importance de regarder à travers les domaines de recherche, car des parallèles frappants peuvent être observés entre le comportement animal et la recherche linguistique lorsqu'on aborde les origines de la complexité de la communication, que ce soit sous la forme du langage humain ou de la communication animale.

General Introduction

The term communication finds its roots in the Latin verb "communicare", formed from the noun "communis" (common, public, or general) meaning to share, to make common, to impart (Harper 2001a). Looking around, one can only be astonished by the incredible variety of shapes communication takes across animal species. If this astounding multiplicity of communicative forms triggered early interest in the first naturalists, it has been a source of constant amazement across time. From the famous discoveries by the ethologist Karl von Frisch, who revealed the waggle dance of honey bees (*Apis mellifera,* von Frisch 1967), to the deafening close-range mating call of the white bellbird (*Procnias albus,* Podos and Cohn-Haft 2019), impressive examples of animal communication continue to capture the interest of scientists. Diversification of communicative systems - each of which being associated with particular sensory systems, signals, and signaling behaviors - has been traditionally recognized to be influenced by phylogenetic history, genetic drift, environmental factors, and sexual selection (Simmons et al. 2003; Ord and Garcia-Porta 2012; Charlton et al. 2012; Maciej et al. 2013).

Nevertheless, communication is first and foremost a means by which individuals build social bonds and assure coordination and regulation of these social relationships (Bradbury and Vehrencamp 2011; Roberts and Roberts 2020). For this reason, several (not mutually exclusive) hypotheses emphasize that the role of a species social environment and its associated socio-cognitive needs may also be determinant to explain signal diversification. These hypotheses were recently nicely synthesized by Dunbar and Shultz (2017) and Freeberg and colleagues (2019) and are here illustrated in Figure 1. Two of these hypotheses are rather specific. First, the “behavioral coordination hypothesis” suggests that sociality is associated with an increasing need for coordination in some particular social context (e.g., social hunting or cooperative breeding). To facilitate this coordination, these specific contexts are expected to constitute selective pressures for increased perceptive abilities associated with more stereotyped signals. Second, the “mate bonding hypothesis” suggests that maintaining long-term pair bonds is especially cognitively demanding. In this context, selective pressures associated with social monogamy are expected to select for the evolution of specific signals and perceptive abilities used in this domain. A third hypothesis, “the Machiavellian intelligence hypothesis” is based on the idea that individuals living in groups will need to balance costs and benefits when confronted with opposite individual and group interests. This hypothesis posits that individuals will then evolve better capacities to alter the behavior of others through cognitive enhancement (e.g., increased memory or inhibitory control) (Whiten and Byrne 1988; Dunbar 1998).

Indeed, increased social cognition will enhance the ability of an individual to behave in cooperative or competitive ways with the members of his group (Freeberg et al. 2019). The “Machiavellian intelligence hypothesis” originally addressed both competitive and cooperative aspects; however, Lucas and colleagues (2018) recently highlighted that different predictions may be derived from these two approaches. On the one hand, competitive and deceptive contexts are expected to favor the evolution of more stereotyped signals. On the other hand, the “social brain hypothesis” predicts that the need for cooperative and prosocial behavior in group-living species would select for more diverse and flexible signals. Cognitively complex communication being assumed to be more effective in forming and maintaining social relationships than non-cognitively complex communication (Roberts and Roberts 2020). Already in 1809, we could read in Jean-Baptiste de Lamarck famous work entitled "Philosophie zoologique":

> *« Les individus […] ayant considérablement augmenté leurs besoins à mesure que les sociétés qu'ils y formaient devenaient plus nombreuses, ont dû pareillement multiplier leurs idées et par la suite ressentir le besoin de les communiquer à leurs semblables. On conçoit qu'il en sera résulté pour eux la nécessité d'augmenter et de varier en même proportions les signes propres à la communication de ces idées. […] Il est donc évident que les individus […] auront dû faire des efforts continuels […] pour créer, multiplier et varier suffisamment les signes que leurs idées et leurs besoins nombreux rendaient nécessaires » (*p344-345, Lamarck 1873)

> [*« The individuals […], having largely increased their needs according as the societies which they formed became larger, had to multiply their ideas to an equivalent extent, and thus felt the need for communicating them to their fellows. I may imagine that this will have compelled them to increase and vary in the same degree the signs which they used for communicating these ideas; hence it is clear that the individuals […] must have made constant efforts, and turned all their resources towards the creation, multiplication and adequate variation of the signs made necessary by their ideas and numerous wants. »* (p172, Lamarck 1963)]

While Lamarck links the evolution of more diverse signals to an increase in the need to communicate in larger communities, other authors, as Peter Marler, emphasize the importance of these signals in cooperative relationships:

> *« Communicative behavior will be of paramount importance in achieving and modulating cooperative relationships. Thus, the genetic makeup of a typical social group is likely to bear on the degree of elaboration that the communicative system of a species exhibits. The most advanced accomplishments should evolve in animals whose societies are so constructed that groups of very close genetic relatives live together in social contact. »* (p48, Marler 1977b)

It is worth noting that historically, the different predictions and theories highlighting a direct relationship between social complexity and communication abilities are based on different approaches to the term communication. First, communication may be seen as a way to communicate emotional or motivational states (Darwin 1872). Emotional states being considered to change over time based on internal or external triggers as energetical level, maturation, or the interactions an individual has (emotional mediation) (Aureli and Schino 2019). Second, communication may be seen as triggered by a need to transfer information, as described by Lamarck (1873). Communication may in this case either be considered in its broad sense as a transfer of information from a sender to a receiver (Bradbury and Vehrencamp 2011) or might be restricted to signals that achieve fitness-enhancing ends by influencing the behavior of others (Owings et al. 1998). The Machiavellian intelligence hypothesis particularly refers to this capacity of an individual to alter the behavior of others (Whiten and Byrne 1988; Dunbar 1998). Hence, animals may either be motivated by anticipating the benefits of a long-term relationship or may interact with others based on their past interactions, being able to respond appropriately to the actions of their partners (Aureli and Schino 2019).

Compiling mentions of the importance of sociality in the evolution of complex communicative systems, we can see that different predictions have been drawn. These predictions are essentially based on two key mechanisms at play in mediating social relationships: individual recognition and social affiliation (Freeberg et al. 2019; Roberts and Roberts 2020).

First, an increase in social complexity results in greater uncertainty in terms of the diversity of individuals an individual may interact with (Freeberg et al. 2012a; Gero et al. 2016; Figure 1). This uncertainty is expected to drive selection for social signals mediating social recognition allowing individuals to interact effectively and efficiently (Gero et al. 2016; Lucas et al. 2018). Recognition may take place at different levels. Acoustic coding of group identity, meaning "vocal convergence" among non-kin adults of one group sometimes associated with "vocal divergence" between neighboring groups (Simmons et al. 2003), was shown to permit group recognition and to maintain group cohesion (Simmons et al. 2003; Tyack 2008). Affiliative or mating association between two individuals can also result in call or song matching effects (convergence). Moreover, vocalizations can also become more distinct, to serve individual recognition, for example. Hence, if individual recognition is essential, individualistic signatures are susceptible to evolve with group size. The more group members are to interact, the more they may benefit to recognize accurately the sender identity of a signal but the more the number of individuals that must be discriminated increases, the more the recognition task is difficult (Pollard and Blumstein 2011). Individuals may need to recognize and discriminate individuals based on only one or several key characteristics (e.g., sex, age, dominance status, group membership, individuality) (Tumulty and Sheehan 2020). For instance, parents from the sub-social burying beetle (*Nicrophorus vespilloides*) only discriminate their larvae based on their age. If external larvae are experimentally introduced in the nest, the parents do not reject them on the condition that these larvae have the same age (Leonhardt et al. 2016). Moreover, individuals may be categorized based on either uniform signals (e.g., cuticular hydrocarbons used for caste recognition in ants; Tumulty and Sheehan 2020) or distinctive individual traits that are associated with a social category by a specific receiver (e.g., individual visual traits in the paper wasp Polistes; Leonhardt et al. 2016). Tumulty and Sheehan (2020) also propose an interesting distinction based on the level of agreement between different receivers. Some characteristics will be attributed uniformly to a given individual by all receivers (e.g., sex, age, species, or caste) while some others, said egocentric, will depend on the specific relationship of this individual with the receiver (e.g., mate, dominant, kin, neighbor; Tumulty and Sheehan 2020). Another level of complexity is added when this category (e.g., dominance status) or when the signals or cues associated with a category (e.g., cuticular hydrocarbon composition in ants) change over time (Leonhardt et al. 2016; Tumulty and Sheehan 2020). Finally, the degree of complexity faced by an individual is increased when it needs to take into account several categories (Bergman and Beehner 2015; Aureli and Schino 2019; Tumulty and Sheehan 2020). Opposing forces may then exist between the need for uniformity and individuality at different levels. These opposing forces may result in the evolution of flexible or multicomponent (e.g., multimodal) signals (Tumulty and Sheehan 2020). Understanding how individuals differentiate and categorize their congeners is hence directly linked to the signaling complexity and diversity across social systems (Shultz and Gersick 2016).

Second, in social groups, individuals are also exposed to greater uncertainty in terms of interaction contexts (Figure 1). In this way, the "call social function hypothesis" proposes that the level of gradation (level of overlap in temporal and acoustic features) of a call type will be influenced by its social function (Snowdon et al. 1997; Griebel and Oller 2008; Lemasson and Hausberger 2011; Bouchet et al. 2013; Keenan et al. 2013). Contact vocalizations are used to maintain group cohesion, spatial separation of group members and to coordinate group movements (McComb and Reby 2005; Fichtel and Manser 2010; Taylor and Reby 2010; Boinski and Mitchell 2010; Pflüger and Fichtel 2012; Charlton et al. 2012; Bouchet et al. 2013; Lemasson et al. 2014). Contact calls are expected to be selected for a higher level of acoustic variability, variability permitting to code reliable information about the caller's identity (inter-individual variability) or the context of emission (intra-individual variability) (Snowdon et al. 1997; Bouchet et al. 2013; Lemasson et al. 2014). Owren and Rendall (2001) nuanced the "call social function hypothesis" by giving more importance to the affective value of the calls. Indeed, evidence was found for a higher level of individual distinctiveness in affiliative calls compared with distress, alarm, or courtship calls (Lemasson and Hausberger 2011; Bouchet et al. 2013). In female Campbell monkeys (*Cercopithecus campbelli*), the greatest gradation level was found in calls associated with the highest affiliative social value whereas, calls associated with agonism were the most stereotyped, and less social alarm calls were intermediate (Lemasson and Hausberger 2011).

Third, group-living individuals usually interact with more and a broader diversity of social partners, ultimately triggering needs to transmit a broader diversity of messages and to express a wider range of emotional and motivational states (Darwin 1872; Lamarck 1873; Morton 1977; Freeberg et al. 2012a; Ord and Garcia-Porta 2012; Figure 1). Because the amount and precision of information that can be conveyed depend on communicative diversity and flexibility, the latest is expected to evolve when social complexity increases. Moreover, the term "communication network" has emerged based on the fact that in many social groups, individuals are closely spaced, signals being able to encompass several signalers and receivers (McGregor and Peake 2000; McComb and Reby 2005; Fichtel and Manser 2010; Pollard and Blumstein 2012 Figure 1). A network environment creates costs and benefits for the receivers. On one hand, it will be more difficult to discriminate information from one individual when several individuals simultaneously communicate (McGregor and Peake 2000). On the other hand, individuals of the social network will be given the possibility of eavesdropping, that is extracting information from signaling interactions between others (McGregor 2005; Fichtel and Manser 2010). As conspicuous signals can draw the attention of unwanted receivers, it constitutes costs for the sender, and specializations are required to direct a signal towards a specific receiver (McGregor and Peake 2000; Freeberg et al. 2012a). Hence, group living individuals will need to monitor and manage the behavior of their group members (Freeberg et al. 2012a; Lucas et al. 2018). They particularly need to integrate information about the frequency, duration, and consequences of different types of interactions with each of their partners (Aureli and Schino 2019). To recognize and remember these past interactions and to subtly assess and manage the behavior of the others, group-living individuals will need increased social cognitive processing abilities, thereby increasing the need for communicative complexity (Freeberg et al. 2012a; Lucas et al. 2018). For instance, in the presence of a potential receiver matching or surpassing their aggressor's rank, chimpanzees victim of attacks appear to produce screams that significantly exaggerated the actual level of aggression experienced (Slocombe and Zuberbuhler 2007).

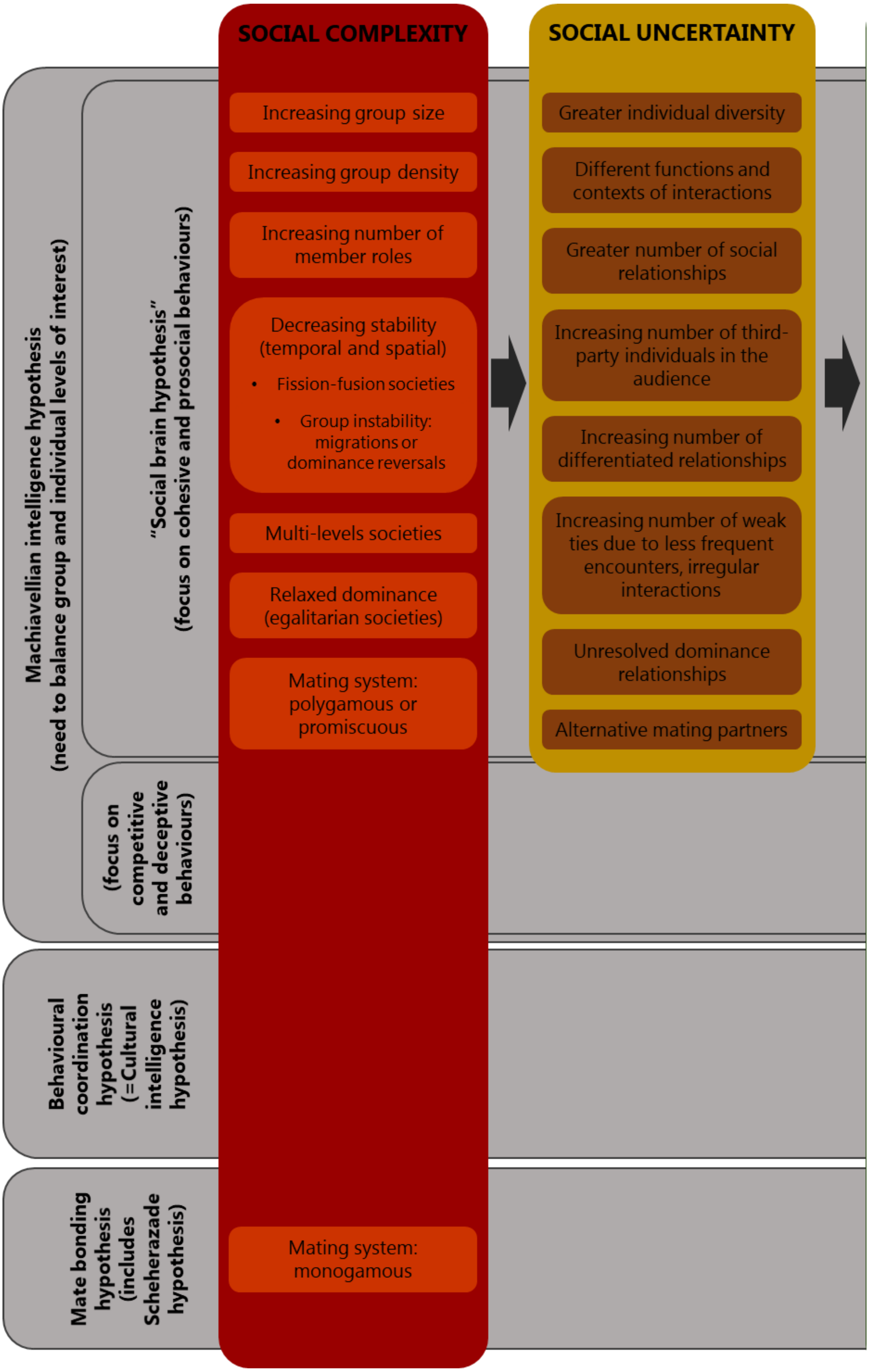
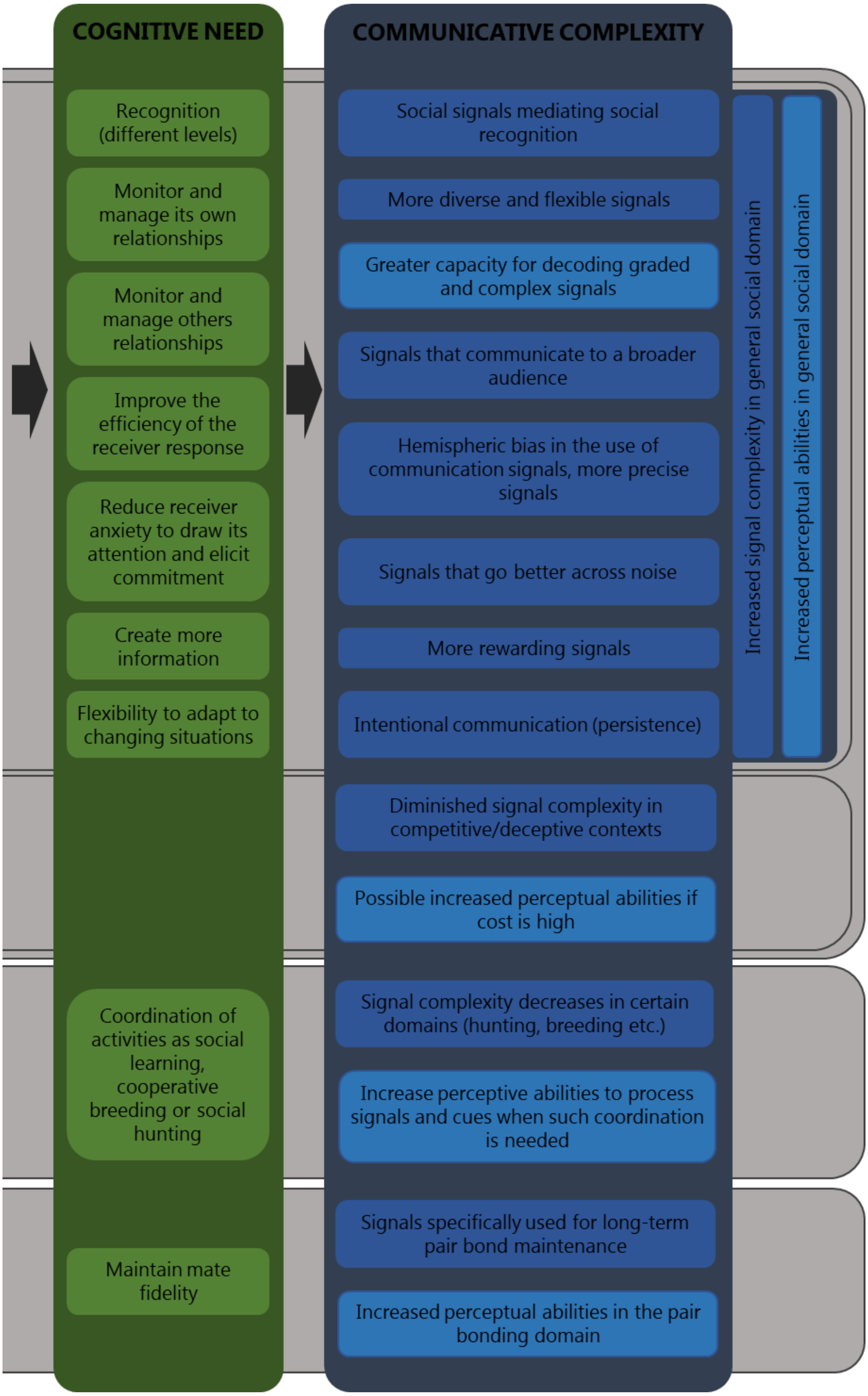


Figure 1: Illustrative summary of the different hypotheses and predictions linking social, cognitive and communicative variables based on Freeberg et al. (2019), Roberts and Roberts (2020). Continues on the next page.


COGNITIVE NEED
Recognition (different levels)
Monitor and manage its own relationships
Monitor and manage others relationships
Improve the efficiency of the receiver response
Reduce receiver anxiety to draw its attention and elicit commitment
Create more information
Flexibility to adapt to changing situations
Coordination of activities as social learning, cooperative breeding or social hunting
Maintain mate fidelity
COMMUNICATIVE COMPLEXITY
Social signals mediating social recognition
More diverse and flexible signals
Greater capacity for decoding graded and complex signals
Signals that communicate to a broader audience
Hemispheric bias in the use of communication signals, more precise signals
Signals that go better across noise
More rewarding signals
Intentional communication (persistence)
Diminished signal complexity in competitive/deceptive contexts
Possible increased perceptual abilities if cost is high
Signal complexity decreases in certain domains (hunting, breeding etc.)
Increase perceptive abilities to process signals and cues when such coordination is needed
Signals specifically used for long-term pair bond maintenance
Increased perceptual abilities in the pair bonding domain
Increased signal complexity in general social domain
Increased perceptual abilities in general social domain

Fourth, social instability as regular changes in dominance structure and fission-fusion dynamics also introduce uncertainty about social relationships triggering a greater need for sensitivity to changes in the social context and the ability to adjust signal use quickly in light of these changes (Freeberg et al. 2012a; Cheney and Seyfarth 2018; Lucas et al. 2018; Aureli and Schino 2019; Figure 1). For instance, baboons were shown to grunt when approaching an individual with which a certain level of uncertainty exists in the relationship (e.g., interactions between sisters) but not when approaching a close-bond partner (e.g., daughter-mother interactions). Grunts are interpreted as social facilitators since they indicate peaceful intentions (Cheney and Seyfarth 2018).

If the idea of a direct link between sociality and the evolution of more complex communicative systems repeatedly appeared in numerous texts and across different disciplines over history (see Freeberg et al. 2012a and Roberts and Roberts 2020 for more on a historical perspective of the question), Blumstein and Armitage (1997) were the first to explicitly test the hypothesis that sociality drives the evolution of communicative complexity. They found, across 22 species of ground-dwelling sciurids, a positive relationship between a social complexity index, based on information theory and considering the diversity of social roles within groups, and the number of distinct alarm calls each species possessed. Following this work, a rebound of interest in the relationship between sociality and signal diversification was observed in the last decade, especially since Freeberg et al. (2012a) formalized the hypothesis as the "Social Complexity Hypothesis for Communicative Complexity" (abbreviated SCHCC in the rest of this work). In this paper, the authors reviewed the evidence in support of the SCHCC and discussed some key limitations to these tests. Building on this framework, I first provide in chapter I, entitled "Clarifying and expanding the social complexity hypothesis for communicative complexity" (Peckre et al. 2019), an updated review of the literature testing the SCHCC (Table I.S1). I also point out and discuss what I believe are still weaknesses and what I identified as the main gaps in the current state of the art concerning these tests of the SCHCC.

If formalizing the SCHCC hypothesis in these terms was indubitably beneficial by providing a framework for future studies, it also generated a necessary confrontation with definitional issues. Indeed, if the term "complexity" is omnipresent in scientific publications, it is generally used with a colloquial sense and interchangeably with other words; as such, it has rarely been defined. Hence, even if some level of discussion started in the 90s about what complexity really is, there is still no general agreement on its definition, neither within nor among disciplines (McShea 1991, 2016; Adami 2002; Bennett 2003). In biology, following

Rudolph Carnap's topology, we more frequently use the term complexity as a comparative concept rather than a classificatory one (Neco et al. 2018). Indeed, we are usually more interested to compare structures, organisms, societies to each other on a relative scale than to state that these are or are not complex in themselves (Neco et al. 2018). But, as science develops and as predicted by Carnap, more quantitative tools should be used to improve objectivity (McShea 2016; Neco et al. 2018). Complexity, in its broad colloquial sense, appears not to be an objective measurable variable (McShea 2016), but its etymology opens the door to possible operational definitions. McShea (1991) stated that "Complexity has to do with number of different kinds of parts and the irregularity of their arrangement" which directly refers to the two Latin roots of the word "complexity" *com* (together) and *plectere* (woven, plaited, twined, entwined) (Harper 2018). Alongside this etymology, a distinction is traditionally made between vertical complexity (also called hierarchical complexity) based on the number of entities of a system and horizontal complexity based on the number of part types (when the variation is discrete) or the degree of differentiation among parts (when the variation is continuous) in that system (Sterelny 1999; McShea 2016). Vertical complexity makes a distinction between a unicellular organism and a multi-cellular one, but it does not consider the individuation of the entities and would not distinguish an assemblage of identical cells from a highly individuated multicellular organism. Comparatively, vertical complexity would not distinguish between a communal-breeding colony of insects and a colony of eusocial insects organized in castes (Leonhardt et al. 2016). This distinction was especially important to contribute to the debate on whether the history of life has been a history of increasing complexity or not (McShea 1991, 2016; Sterelny 1999). For Gould, this trend seems to be only a spread of variation, most of the organisms remaining simple forms but some extreme cases appearing (Sterelny 1999). This is consistent also with the idea of the Zero Force Evolutionary Law (ZEFL) stating that complexity tends to increase in the absence of forces, as a passive trend (Sterelny 1999; McShea 2016). For Maynard Smith and Szathmary, on the contrary, there is an inherent directionality with shifts in complexity (Sterelny 1999). McShea, however, argues that these shifts are addressing different levels of complexity. Some of these shifts correspond to horizontal complexity, with the notion of increasing heterogeneity in the number and arrangements of parts (e.g., the transition from RNA acting as both replicator and enzymes to protein-mediated DNA replication), while some other shifts correspond to vertical complexity, addressing the question of the number of layers in a system (e.g., the transition from solitary individuals to colonies).

This distinction between vertical and horizontal complexity emphasizes the importance of considering the scale to which complexity is considered (Sterelny 1999; Peckre et al. 2019; Hobson et al. 2019). In a free-living single-cell species, a protist, every cell must be omnipotent while as differentiation proceeds, cells diversify into distinct types and become specialized for particular functions (McShea 2016). Similarly, among the social insects, the larger, more individuated colonies with a greater number of castes have more specialized individuals than smaller less-individuated colonies (Anderson and McShea 2001; McShea 2016). Hence, the social complexity emerging from the interactions between group members may not be the same social complexity experienced by the individuals interacting (Leonhardt et al. 2016; Fischer et al. 2017a; Lucas et al. 2018; Aureli and Schino 2019; Hobson et al. 2019). For instance, the presence of social roles limits the range of contexts a single individual will be exposed to reducing the need for diverse and complex signals at the individual level. On the contrary, in absence of social roles, each individual may need to convey information across a variety of contexts requiring higher complexity at the individual level. I further explore this question in chapter II.

Maybe what we should extract out of these last paragraphs is that it is short-sighted to expect that a single approach to complexity will capture all the relevant aspects of the complexity of a system. Complexity should rather be conceptualized and operationalized along multiple axes (Blumstein and Armitage 1997; Neco et al. 2018; Peckre et al. 2019; Hobson et al. 2019). In this sense, many quantitative concepts have been proposed recently to describe the complexity of a system in a more fine-grained comparative way (Neco et al. 2018). Moreover, by adopting a multidimensional approach of complexity, more precise trends may appear. Indeed, different measures of complexity may provide different answers to the predictions drawn with the general term complexity (e.g., complexity increases during evolution, communicative complexity increases with social complexity). Understanding which specific dimensions of communicative complexity are increased in response to which dimensions of social complexity constitutes a set of questions that may be even more informative than the initial one.

As I mentioned earlier, the formulation of the SCHCC in these terms is inevitably dragging along the issues surrounding the term complexity. A specific and urgent need for better tools and concepts to estimate both social and communicative complexity more reliably across taxa arises (Freeberg et al. 2012b; Bergman and Beehner 2015; Fischer et al. 2017a, b; Pika 2017; Nehring and Steiger 2018; Kappeler 2019). In the first part of chapter I, I provide an overview of the current operationalization of the definitions of social and communicative complexity together with new perspectives on the matter. I primarily focus on communicative complexity as it remains poorly studied in these terms whereas social complexity has seen in the last years a flourishing amount of literature (Fischer et al. 2017a;

Kappeler 2019; Weiss et al. 2019; Hobson et al. 2019). I especially argue for the integration of a multimodal approach to communicative complexity.

Human language is an exceedingly complex and intricate behavior that is argued to distinguish humans from the rest of the living world; the question of language's origin being thus regarded as one of the more challenging problems in science (Christiansen and Kirby 2003; Fedurek and Slocombe 2011; Krams et al. 2012). Lamarck himself already mentioned that language may be an extreme case of communicative elaboration resulting from increased social pressures. Indeed in "Philosophie zoologique" he also mentioned:

> *« ayant eu besoin de multiplier les signes, pour communiquer rapidement leurs idées devenues de plus en plus nombreuses, et ne pouvant plus se contenter, ni des signes pantomimiques, ni des inflexions possibles de leur voix, pour représenter cette multitude de signes devenus nécessaires, seront parvenus, par différents efforts, à former des sons articulés […] De là […] l'origine de l'admirable faculté de parler »* (p346, Lamarck 1873)

> [*« stood in need of making many signs, in order rapidly to communicate their ideas, which were always becoming more numerous and could no longer be satisfied either with pantomimic signs or with the various possible vocal inflexions. For supplying the large quantity of signs which had become necessary, they will by various efforts have achieved the formation of articulate sounds. […] Hence would arise […] the marvelous faculty of speaking. »* (p173, Lamarck 1963)]

Language was first suggested to have evolved in humans to facilitate coordination of elaborated tasks as hunting, tool manufacture, or cooking (Cordón 1992; Dunbar 2003). However, Dunbar (2003) further advanced and supported the hypothesis that language rather emerged to serve a social function and only after was used to serve other technological functions. He suggested that language may have originally evolved to serve social relationships once grooming, the conventional social bonding device in primates, became unable to serve this function in larger groups (Dunbar 2003; McComb and Semple 2005; Griebel and Oller 2008; Krams et al. 2012). Language may have allowed modern humans to counter time constraints, "vocal grooming" allowing them to socialize simultaneously with more than one partner at a time and while performing other essential activities such as foraging. Dunbar's "vocal grooming hypothesis" currently still constitutes one of the main theories regarding the origins of human language and may more generally explain variation in systems of vocal communication in animals (Freeberg 2006; Krams et al. 2012; Lemasson et al. 2014). For instance, the pattern of call exchange in ring-tailed lemurs (*Lemur catta*) reflects their affiliative relationships (Oda 2008; Kulahci et al. 2015). If the "vocal grooming hypothesis" suggests that language stemmed from the vocal-auditory modality, it also implies an intimate relationship between communicative modalities (sensory systems with which a signal is produced and perceived by the receiver; Smith and Evans 2013). In this perspective, the discovery of the activation of mirror neurons linked to both hand and mouth gestures in homologous language areas of the monkey brain has further led to the gestural theory of language evolution. This theory offers gestures as the most promising precursor of language (Corballis 2002; Arbib 2005; Gentilucci and Corballis 2006; Slocombe 2011). Hand gestures may have been turned to mouth gestures until a point when hand gestures were occulted, hands serving other activities (Corballis 2002). This gestural theory of language is mainly based on the evidence of the existence of large and flexible gesture repertoires in great apes, the latest having highly genetically constrained vocal repertoires.

However, *de facto*, visual and vocal communicative signals are, even in humans, rather than exclusive, usually produced in combination (Mcgurk and Macdonald 1976; Gustison and Bergman 2017). Hence, rather than a signal generated in a single modality, multimodal communication may be the entry point for human language flexibility (Waal and Pollick 2011; Leavens et al. 2014; Wilke et al. 2017). In this sense, the multimodal theory of language suggests that language results from the coevolution between gestural, vocal, and oro-facial communication modalities. In this context, the bimodal speech rhythm hypothesis suggests, for instance, that some primate rhythmic facial expressions like lip-smacking set the stage for fast-paced vocalizations that would later become speech (Ghazanfar 2013; Gustison and Bergman 2017). This notwithstanding, Slocombe and colleagues (2011) reported that only 5% of the studies on primate communication conducted between 1960 and 2008 adopted a multimodal approach. Integrated multimodal research appears today as utterly needed to appreciate better the potential selective pressures leading up to language and more generally signals evolution (Slocombe et al. 2011; Liebal et al. 2013; Waller et al. 2013).

Additionally, while the comparative approach consisting of looking at precursors of language in other animal species and especially other primate species is widespread, there is still no definite distinction between humans and non-human animals' communication (Gustison and Bergman 2017; Prat 2019). Indeed, some characteristics historically considered to be particular of language were found in other animals too. So, there is still a need for more studies on non-human animal communication to differentiate better the features that are unique to human speech (Gustison and Bergman 2017). Moreover, comparisons deal with parallels between human speech and other animals' vocal communication (reviewed in Leavens et al. 2014; Prat 2019), the other vocal communication productions of humans being usually ignored and the analytical methods differing between studies in humans compared to other animals (Anikin et al. 2018; Prat 2019).

Interestingly, linguistic research has, in parallel to studies on non-human animal communication, tried to understand the sources for language diversity. In striking contrast with the SCHCC, larger human communities have been predicted to have evolved less complex languages (fewer and less elaborate morphological structures, fewer irregulars, and overall simpler grammars) to ease generalizations and transparency (Lupyan and Dale 2010; Perry et al. 2010; Nettle 2012; Lev-Ari 2016, 2018; Raviv et al. 2019). This prediction appears in opposition with the SCHCC, as we have seen that in this framework larger groups are predicted to constitute selective pressures for the evolution of more complex communication systems. This contradiction reveals an approach closer to the one adopted by the "behavioral coordination hypothesis" (Figure 1) suggesting that if language evolved as a means for social coordination, coordination may be facilitated by more stereotyped signals. However, this contradiction may also reflect different approaches and definitions of communicative complexity across fields.

Indeed, the variation of language complexity has been described in two different dimensions, syntagmatic and paradigmatic complexity (Sinnemäki 2011; Nettle 2012), echoing the two concepts of horizontal and vertical complexity introduced earlier (McShea 2016). The syntagmatic complexity describes the number of parts of a linguistic object (e.g., length of words in terms of syllables or morphemes) and recalls the concept of vertical complexity. The paradigmatic complexity, meanwhile, describes the information carried by each unit (e.g., morphological complexity) mirroring the concept of horizontal complexity. The more elements there are to a system, the greater is its syntagmatic complexity, while the greater the variety of the elements in the system is, the greater its paradigmatic complexity. Interestingly, while a robust positive correlation was shown between speaker population size and the size of the phonological inventory, a negative relationship was shown with morphological complexity (reviewed in Nettle 2012). In communities with a smaller speaker population, individuals should be exposed to fewer demonstrators, or more similar ones so would be exposed to less variation. On the contrary, interacting with more people reduces shared history and introduces more input variability, which individuals need to overcome, introducing a more substantial pressure toward generalizations and transparency. Larger communities may favor the evolution of simple, predictable, and structured variants (Perry et al. 2010; Lev-Ari 2016, 2018). Languages of large communities would then have more extensive phonological inventories, shorter words, and lower morphological complexity than the language in smaller communities (Nettle 2012).

Besides human linguistic studies and few studies carried on other animals (Freeberg 2006), the SCHCC has been mainly considered at the inter-specific level. Inter-specific comparisons are of particular interest to reveal the selective pressures at the roots of the currently observed variations between species. However, usually, these studies, in order to include a greater number of species in their analysis, focus on an extremely limited number of parameters. Here I argue that smaller scale comparisons associated with a more holistic description of the complexity of the communicative and social systems will also be highly informative, especially if it permits better control of alternative hypotheses by reducing the variation due to ecology or anatomy, for instance. Moreover, comparisons between phylogenetically closely related species may potentially be more relevant to identify specific social factors leading to greater communicative complexity, in dismissing the differences explained by phylogeny. Indeed, anatomical factors, ecological factors, and neutral or non-adaptive evolutionary processes are all possible non-social pressures that might produce communicative complexity (McComb and Semple 2005; Freeberg et al. 2012a; Ord and Garcia-Porta 2012; Peckre et al. 2019). Hence, any comparative study on communication should include considerations about habitat and morphological differences between species as well as their phylogenetic relationship (Ramsier et al. 2012; Manser et al. 2014). I discuss in more detail these aspects in chapter I (section III.1), chapter II, and chapter IV (section I).

We have built chapters II and III in an effort to bring constructive new perspectives in the tests of the SCHCC and contribute to the picture described above while addressing the issues pointed out in chapter I. These chapters also provide provisional applications of the ideas raised in chapter I. I specifically present in chapter II entitled "A multimodal approach to communicative complexity in two lemur species having different social systems" a comparative analysis of the multimodal communicative systems of mongoose lemurs (*Eulemur mongoz*) and red-fronted lemurs (*Eulemur rufifrons*) and discuss the observed differences regarding the variations in their social systems. I believe that lemurs are especially interesting models for this study. First, by being at the base of the primate tree, they are of special interest in understanding factors driving the evolution of communication in humans and primates in general (Norscia and Palagi 2016a). Although lemurs are conspicuously vocal and use a wide range of vocalizations, their vocal communication systems remain poorly studied (Oda 2008; Gamba et al. 2015). Moreover, they are not only conspicuously vocal but also rely heavily on olfactory communication and have a well-developed visual sense (delBarco-Trillo et al. 2011; delBarco-Trillo and Drea 2014; Rakotonirina et al. 2017). Nevertheless, most previous studies on multimodal communication have been conducted on anthropoid primates (Slocombe et al. 2011; Norscia and Palagi 2016b). As despite their primitive physical characteristics and relatively small brains (Oda 2008), they also have complex social systems, they provide an excellent model to test the SCHCC. Among lemurs, the true lemur genus (*Eulemur*) contains twelve different species all endemic to Madagascar (Markolf and Kappeler 2013). They live in groups of different average sizes (Ossi and Kamilar 2006; Kappeler and Fichtel 2015) and are of special interest in this respect because they constitute one of the rare cases of potential transition from a group-living ancestor to social monogamy (Lukas and Clutton-Brock 2013; Kappeler and Fichtel 2015) offering a unique opportunity to test the effect of the selective pressures associated with this transition. In chapter II and IV (section I) I explain in more detail the relevance of my specific species choice. With the data collected for this study, I also contributed to a project carried out by Dr. Eithne Kavanagh and Pr. Katie Slocombe (Department of Psychology, University of York, UK) resulting in a submitted paper entitled "Dominance style is a key predictor of vocal use and evolution across non-human primates". In chapter IV, entitled "On the look for mongoose lemurs", I additionally expose some technical details and ethical concerns experienced during the choice of my field sites.

In chapter III entitled “Sex differences in the audience effect on anogenital scent-marking in an egalitarian species of lemur, the red-fronted lemur” I specifically address an additional issue raised in chapter I (section III.2). I note that looking for the potential effects of social complexity on communicative complexity, researchers rarely address the actual ways in which variation in signaling is directly affected by social factors (Gustison et al. 2012). The way an individual will communicate can indeed be also modified either in a large time-scale by the social environment, here defined as "the individuals an individual is frequently in contact with" or in a shorter time-scale by the social context, here defined as "the nature or status of the individuals present in the signal range of a sender" (Slocombe and Zuberbuhler 2007; Fichtel and Manser 2010; Pflüger and Fichtel 2012; Kalan and Boesch 2015). In this chapter III, I specifically provide an illustration of a specific perspective proposed in chapter I (section III.2.b). In this study, I indeed investigated the existence of potential intragroup audience effects on anogenital scent-marking behaviors in a wild population of red-fronted lemurs. I particularly investigated whether males and females differed in this aspect and if these differences may reveal functional dissimilarities associated with anogenital scent-marking across sexes. Studying the flexibility of usage of complex signals, as multimodal signals, across social contexts (i.e., audiences), this work also contributes to uncovering potential social selective pressures that may have led to the evolution of flexible signals.

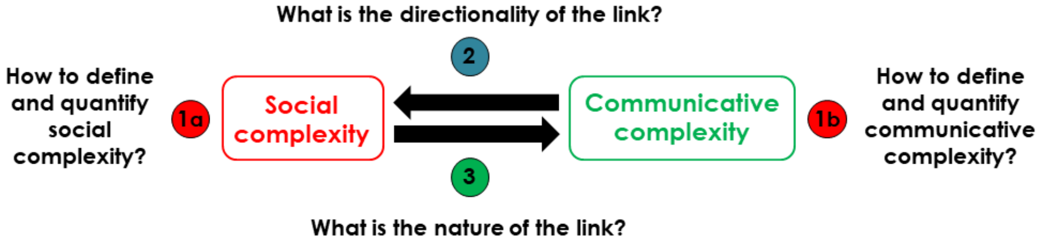
Finally, in chapter V entitled "Remotely releasable collar mechanism for medium-sized mammals: an affordable technology to avoid multiple captures" (Buil and Peckre et al. 2019), I present a work developed in collaboration with the Neurobiology Laboratory (German Primate Center, Göttingen, Germany) with the aim of attaching small recorders to collars. Recording lemur vocalization using this technology may have allowed more accurate call rate estimations, better quality recordings (Couchoux et al. 2015), and would have allowed us to record simultaneously vocalizations and other behaviors with a single observator. However, although such technology may represent an improvement in terms of data quality it is at cost as it requires capturing animals. Captures still imply several risks and costs for the animal. Hence, we have tried to develop a releasable collar system that was successfully tested in field-like conditions on two ring-tailed lemurs (*Lemur catta*) housed in the Wildlife Park Affenwald (Germany). As this work was carried out in parallel, this method was not used to acquire the data presented in chapter II.

Additionally, in a supplementary chapter entitled "Potential self-medication using millipede secretions in red-fronted lemurs: combining anointment and ingestion for a joint action against gastrointestinal parasites?" (Peckre et al. 2018), I present a side project born from field observations on the red-fronted lemurs.

Thesis outline

Chapter I:

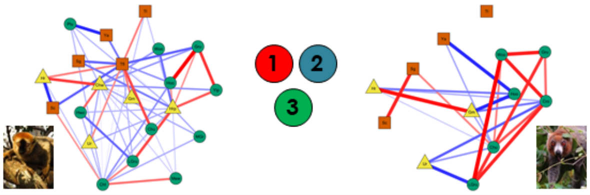
Clarifying and expanding the social complexity hypothesis for communicative complexity



Peckre et al. 2019 *Behav. Ecol. Sociobiol.*

Chapter II:

A multimodal approach to communicative complexity in two lemur species having different social systems



Chapter IV:

On the look for mongoose lemurs

Chapter III:

Sex differences in the audience effect on anogenital scent-marking in an egalitarian species of lemur, the red-fronted lemurs

Peckre et al. to be submitted

Chapter V:

Remotely releasable collar mechanism for medium-sized mammals: an affordable technology to avoid multiple captures

Buil & Peckre et al. 2019 *Wildlife Biol.*

Supplementary Chapter :

Potential self medication using millipede secretions in red fronted lemurs: combining anointment and ingestion for a joint action against gastrointestinal parasites?

Peckre et al. 2018 *Primates*

Chapter I: Clarifying and expanding the social complexity hypothesis for communicative complexity

A review paper in Behavioral Ecology and Sociobiology (accepted in November 2018)

Contributions (following CRediT taxonomy): Conceptualization, L.R.P., C.F, and P.M.K.; Methodology, L.R.P.; Writing – original draft preparation, L.R.P.; Writing – review and editing, L.R.P, L.S.M., C.F., and P.M.K.; Visualization, L.R.P.; Supervision, C.F., and P.M.K.; Funding acquisition, L.R.P., C.F, and P.M.K.

Abstract – Variation in communicative complexity has been conceptually and empirically attributed to social complexity, with animals living in more complex social environments exhibiting more signals and/or more complex signals than animals living in simpler social environments. As compelling as studies highlighting a link between social and communicative variables are, this hypothesis remains challenged by operational problems, contrasting results, and several weaknesses of the associated tests. Specifically, how to best operationalize social and communicative complexity remains debated; alternative hypotheses, such as the role of a species' ecology, morphology, or phylogenetic history, have been neglected; and the actual ways in which variation in signaling is directly affected by social factors remain largely unexplored. In this review, we address these three issues and propose an extension of the "social complexity hypothesis for communicative complexity" that resolves and acknowledges the above factors. We specifically argue for integrating the inherently multimodal nature of communication into a more comprehensive framework and for acknowledging the social context of derived signals and the potential of audience effects. By doing so, we believe it will be possible to generate more accurate predictions about which specific social parameters may be responsible for selection on new or more complex signals, as well as to uncover potential adaptive functions that are not necessarily apparent from studying communication in only one modality.

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I. Introduction

Life in stable groups unfailingly entails repeated interactions between different individuals, creating particular costs and benefits for individual group members and the group as a whole. The "social intelligence hypothesis" suggests that increased socio-cognitive skills are necessary to effectively navigate this social network in order to reap the benefits of sociality (Jolly 1966a; Humphrey 1976; Whiten and Byrne 1988; Dunbar 1992). Social competence, which describes the ability to reliably assess the behavior of others and to respond flexibly and adaptively to it, for example by remembering prior interactions, anticipating others' behaviors, and by coordinating one's own behavior with that of other group mates, summarizes the key cognitive abilities that are favored in this context (Cheney and Seyfarth 2005; Dunbar 2009; Taborsky and Oliveira 2012; Sewall 2015). Increased social competence has been suggested to trigger the need for more complex communicative systems, being the key behavioral mechanism mediating these interactions (McComb and Semple 2005; Freeberg 2006; Freeberg et al. 2012b, a; Sewall 2015).

The traditional approach to studying communication is based on the sender-receiver paradigm, i.e., a dyad connected by the transmission of a signal in a particular channel (Shannon and Weaver 1949). More recently, however, it has been recognized that signals may connect several senders and receivers within a group (McGregor and Peake 2000; Cheney and Seyfarth 2005; McComb and Reby 2005; Fichtel and Manser 2010; Pollard and Blumstein 2012). In particular, multiple individuals may communicate simultaneously, and conspicuous signals may draw the attention of unwanted receivers (McGregor and Peake 2000; Peake 2005; Fichtel and Manser 2010). Hence, specific mechanisms are required to direct a signal of a given sender towards a specific receiver (McGregor and Peake 2000; Freeberg et al. 2012a).

Moreover, group-living individuals are usually involved in a wider range of interactions with diverse social partners, ultimately triggering needs to transmit a broader diversity of information and to express a wider range of emotional and motivational states (Morton 1977; Freeberg et al. 2012a; Ord and Garcia-Porta 2012). Accordingly, the "social complexity hypothesis for communicative complexity" (SCHCC) posits that animals living in groups with comparatively greater social complexity will exhibit greater complexity in their signaling systems (Freeberg 2006; Freeberg et al. 2012b, a). This hypothesis formalizes ideas that have been acknowledged ever since Darwin (1872) but that had never been explicitly tested (see Freeberg et al. 2012a) for a historical perspective). Accordingly, the complexity of social groups ought to drive communicative complexity in both a proximate (context for signal development) and ultimate (social selection pressure) sense towards increased signal diversity among species, populations, and groups (Freeberg et al. 2012b; Krams et al. 2012). Empirical evidence from diverse taxa and for three different communicative modalities (auditory, visual, and olfactory) has supported this hypothesis (Table I.S1). However, there are also several studies not reporting the predicted positive relationships (Table I.S2) and the work of Freeberg (2006) seems still to be unique in adopting an experimental approach to test predictions of this hypothesis. Building on influential previous work by Freeberg et al. (2012a, b), in the present paper, we point out new perspectives that significantly expand the existing framework.

Specifically, three key issues have emerged from the recent literature that may offer interesting new perspectives on the SCHCC (Figure I.1). The first issue concerns the operational definition of the main variables (1 and 2 in Figure I.1). Because the unspecified usage of the term complexity can lead to a lack of agreement on the relevant variables, there is a need for better quantitative tools to estimate social and communicative complexity more systematically across taxa (Freeberg et al. 2012a; Bergman and Beehner 2015; Fischer et al. 2017a, b; Kappeler 2019). Secondly, while numerous studies have highlighted a link between social and communicative complexity, their correlative nature does not permit conclusions about the direction of causality (3 in Figure I.1). Hence, a systematic control for alternative hypotheses that invoke important effects of ecology, morphology, or phylogenetic history on communicative complexity appears essential when testing the link between social and communicative complexity. Finally, we note that researchers rarely address the actual ways in which variation in signaling is directly affected by social factors (4 in Figure I.1). Indeed, the underlying mechanisms of this link are usually not explored, failing to uncover the specific attribute of communication that would be co-evolving with specific aspects of sociality (Pollard and Blumstein 2012; Gustison et al. 2012, 2019). In this review, we will address these three crucial issues, taking stock of the current state of the art and point out what we believe are the main associated perspectives. In doing so, we hope to provide guidelines and inspiration for future tests of the SCHCC.

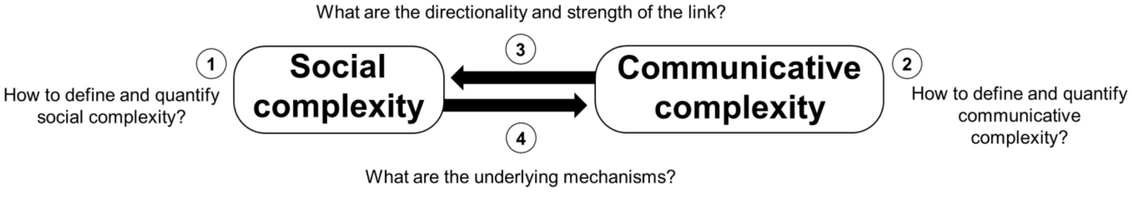


Figure I.1: Schematic representation of three key issues associated with tests of the "social complexity hypothesis for communicative complexity" (SCHCC)

II. What are we looking at? Need for good operational definitions

Whereas the term “complexity” is omnipresent in scientific publications, there is no general agreement on its definition, neither within nor among disciplines (Adami 2002; Bennett 2003). The two Latin roots *com* (together) and *plectere* (woven, plaited, twined, entwined) (Harper 2018) indicate that multiple parts are connected to each other in flexible ways. Pollard and Blumstein (2012) accordingly suggested that “a system is typically considered more complex if it contains more parts, more variability or types of parts, more connections or types of connections between parts or more layers of embedded meaning”. This verbal definition, though helpful, does not offer any operational criteria to evaluate social and communicative complexity, but highlights the importance of a holistic approach (Freeberg et al. 2012a). Hence, there is currently a need for better tools and concepts to estimate both social and communicative complexity more reliably across taxa (Freeberg et al. 2012b; Bergman and Beehner 2015; Fischer et al. 2017a, b; Pika 2017; Kappeler 2019).

Another issue when trying to define and quantify social and communicative complexity in the context of the SCHCC concerns the non-independence between communication and sociality that may even amount to circularity. If social complexity is measured through communicative interactions or communicative complexity through its social outcomes, then we should not be surprised to find correlations between these variables. An analogous problem exists between sociality and cognition, leading Bergman and Beehner (2015) to suggest to measure social cognition in a different context than the chosen measure of social complexity. In addition, communication, together with social interactions, constitutes the core of a species’ social structure (Kappeler 2019). Hence, measures thereof that are correlated with measures of social organization, such as group size, may therefore reduce the risk of redundancy and non-independence, and this is what several studies effectively did (e.g., (Blumstein and Armitage 1997; McComb and Semple 2005). However, this approach can and has been criticized on the grounds that measures of social organization (notably group size) alone do not fully capture all relevant dimensions of social complexity (Shultz and Dunbar 2010; Kappeler 2019). Thus, comprehensive measures of social complexity, in particular, need to be developed (Kappeler 2019).

1. Social complexity: developing broadly applicable quantitative measures.

The main variable used to assess social complexity in the context of the SCHCC has been group size (Table I.S1and Table I.S2). Some studies have used various derived or more specific measures for sub-units (e.g., foraging group, grooming clique, or group density), but all of them are based on the notion that individuals in larger units are expected to interact with more partners, triggering a need to convey more diverse and flexible messages (Freeberg et al. 2012a). Group size is a convenient proxy of social complexity as it is relatively easy to assess for large numbers of species, but it is commonly recognized as only a crude measure of social complexity (McComb and Semple 2005; Shultz and Dunbar 2007; Freeberg et al. 2012a; Bergman and Beehner 2015). Indeed, even if group size is undeniably a key determinant of social complexity (Kappeler 2019) and has been shown to be a good proxy for social complexity in some taxa (Bourke 1999; Jeanson et al. 2007), it may fail to capture differences in social complexity, especially across taxa. For example, a herd of ungulates, a troop of baboons and a colony of ants may be constituted of the same number of individuals, but no one in the field would consider them as equally socially complex.

Because the notion of complexity is not only based on the number of units but also on the connections between these parts (Pollard and Blumstein 2012; Freeberg et al. 2012a), some studies considered other social features, such as mating system, dominance style, or breeding strategies, as better or alternative proxies of social complexity. However, some of these alternative classifications have themselves been questioned, and their ranking can be controversial and largely dependent on the taxa considered (Kappeler 2019). For example, pair-living species may be considered as the simplest form of social complexity because they have the smallest group size, but this type of social system typically also includes long term bonds that require familiarity and a subtle coordination of each other's behavior. In some taxa, they have therefore been considered as a very complex form of sociality (ungulates: Shultz and Dunbar 2007; bats: Pitnick et al. 2006), whereas in others certain pair-living species have been characterized as the baseline of social complexity (primates: Dröscher and Kappeler 2013).

Similarly, regarding the patterns of group-level dominance relationships, there is no agreement on which pattern is more socially complex. Some authors argued that linear dominance hierarchies are socially more complex than egalitarian ones because they require particular cognitive abilities, such as transitive inference (MacLean et al. 2008).

However, non-linear hierarchies could equally be considered as more complex, especially from the animal's perspective, as they represent more uncertainty and necessitate more social competence (Taborsky and Oliveira 2012). Hence, it is important to clarify the level of analysis; whereas some studies address complexity at the group level, others focus on the individual level, resulting in divergent interpretations (Aureli and Schino 2019).

The ranking of social features in terms of social complexity may also be prone to circularity because social complexity is usually evaluated with regard to the number of cognitive skills or the type and frequency of communicative interactions. Hence, the usage of particular social features may not solve the definitional problem and may even enhance subjectivity. Against this background, the verbal definition by Freeberg et al. (Freeberg et al. 2012a), who defined "complex social systems are those in which individuals frequently interact in many different contexts with many different individuals, and often repeatedly interact with many of the same individuals over time," represents important progress. More recently, Bergman and Beehner (2015) suggested to measure social complexity as the "number of differentiated relationships that individuals have". These verbal definitions, although non-operational, are essential pre-requisites for the development of meaningful quantitative measures, at least of variation in aspects of social structure, such as the one proposed by Fischer et al. (Fischer et al. 2017a) based on several common social indices and cluster analysis, or the one offered by Weiss et al. (Weiss et al. 2019) applying binomial mixture models to association indices.

Facing this diversity of social complexity measures, it is evident that this concept encompasses different aspects and that a single measure may not be sufficient to assess it globally. Hence, a better appreciation of the complexity of a social system may rather be provided by a set of operational measures describing all of the four fundamental aspects proposed by Kappeler (Kappeler 2019), i.e., social organization, social structure, mating system, and care system (Table I.1). This systematic approach may facilitate progress with future comparative studies in this domain.

Hence, we believe that in the context of the SCHCC, more effort needs to be invested into the choice and definition of the variables used to assess social complexity. In particular, favoring broadly applicable quantitative measures rather than subjective categories should facilitate comparative work and clarify the level at which complexity is evaluated (Weiss et al. 2019). Moreover, measures implicitly based on communicative variables should be avoided in order to stave off circularity. Rather than a single measure, we propose that a set of operational measures matching the criterion mentioned above and accounting for all four main components of social complexity (Kappeler 2019) will help to move the field forward. Better identifying the social complexity aspects included in the test should also allow for better predictions and understanding of the mechanisms underlying the observed relationship (see below).

2. Communicative complexity: from partitioning signals towards a systematic multimodal approach

One of the main issues associated with communicative complexity results from the partitioning of the distinct modalities in which signals are produced. Each signaling modality, defined as the sensory system with which a signal is produced and perceived by the receiver (Smith and Evans 2013), has historically been highlighted in different taxa. This bias has led to the development of different research questions, approaches, and methodologies across these different modalities (Liebal et al. 2013). Our own sensory bias, together with differences in the ease of data collection and unequal development of technological tools, have resulted in large biases in the number of studies between the different modalities.

In the context of the SCHCC, but also more generally in communication research, mainly the auditory, olfactory, and visual modalities have been explored, with a strong bias towards acoustic communication (Baptista and Gaunt 1994; Slocombe 2011). Its universality and the fact that most species produce acoustic signals easily perceptible by humans may explain this bias. Indeed, because many olfactory signals are not easily perceived by humans, more sophisticated analytical methods are required to study them in more detail. Only a few studies have addressed the complexity of these signals and even fewer from a comparative perspective (Kather and Martin 2015). Visual signals are highly diverse because they can be produced by completely different processes, such as movements of the whole body or body parts (e.g., foot-flagging of some frogs) as well as changes in coloration or shape (e.g., feather erection display of birds), making it difficult to define broadly applicable measures of visual signal complexity (Endler 1992; Cuthill et al. 2017). Moreover, visual signals vary widely in persistence, ranging from state signals, such as static features of coloration patterns, to dynamic signals with limited duration that require an action by the signaler to be initiated (Smith and Evans 2013).

Table I.1: Summary of the different social and communicative variables used to test the SCHCC in different taxa and modalities.

		Social variables	Communicative variables	References
Birds	Auditory	**Social organization** • Group/colony size **Social structure** • Cohesiveness of social bonds • Between group competition **Mating system** • Mating system • Extra-pair paternity **Care system** • Cooperative breeding (yes/no) • Communal breeding (yes/no)	**Number of signaling units** • Vocal repertoire size • Syllable repertoire size • Song repertoire size **Uncertainty – combinations** • Diversity of notes and notes pairings (uncertainty index) **Uncertainty – gradation** • Potential for individuality coding • Individuality in chick begging calls	(Kroodsma 2004); (Medvin et al. 1993); (Mathevon et al. 2003); (Freeberg 2006); (Ord and Garcia-Porta 2012); (Leighton 2017)
Insects	Olfactory	**Social organization** • Social/solitary • Ancestral solitary, eusocial, secondarily solitary • Colony size **Mating system** • absence/presence of polygyny or polyandry	**Number of signaling units** • Number of chemical classes produced • Density of sensillae • Number of different cuticular hydrocarbons (CHC) • Number of CHC isomers	(Ord and Garcia-Porta 2012); (Kather and Martin 2015); (Wittwer et al. 2017)
	Visual	**Care system** • Nesting strategies flexibility (absence/presence)	**Uncertainty – gradation** • Inter-individual variability in facial and abdominal markings	(Tibbetts 2004)
Mammals	Auditory	**Social organization** • Solitary/pair/group • Group/colony size • Diversity/variability of demographic (age-sex) roles **Social structure** • Female gregariousness • Grooming time • Social affiliative value of the context • Armitage's sociality index • Michener's social grade • Blumstein and Armitage's social complexity index **Mating system** • serial monogamy, promiscuous, or polygamous	**Number of signaling units** • Vocal repertoire size • Adult vocal repertoire size • Repertoire size of adult males • Number of affiliative call types • Alarm call repertoire size • Number of tonal sound inflection points (tonal sound modulation) • Call rate **Uncertainty – combinations** • Diversity index (complexity of the vocal repertoire in terms of "unit assembling pattern" types) **Uncertainty – gradation** • Individuality in infant isolation calls • Amount of individuality in alarm calls • Potential for identity coding • Call coefficient of variation • Call variability **Uncertainty – adaptations** • Mean minimum tonal sound frequency • 60 dB high-frequency limits • Mean auditory brainstem response threshold	(Blumstein and Armitage 1997); (Stirling and Thomas 2003); (Wilkinson 2003); (McComb and Semple 2005); (May-Collado et al. 2007); (Lemasson and Hausberger 2011); (Pollard and Blumstein 2011); (Gustison et al. 2012); (Ramsier et al. 2012); (Bouchet et al. 2013); (Manser et al. 2014); (Vanden Hole et al. 2014); (Zimmermann 2017)

	Olfactory	**Social organization** - Large multi-males-multi-females groups vs. small family groups **Social structure** - Co-dominance vs. female dominance	**Number of signaling units** - Number of chemical compounds in the perianal and genital secretions	(delBarco-Trillo et al. 2012)
	Visual	**Social organization** - Group size	**Number of signaling unit** - Facial color pattern complexity - Number of visually distinct facial movement - Pelage markings - Color pattern complexity = total number of uniquely different color areas on the face	(Dobson 2009); (Santana et al. 2011); (Santana et al. 2012); (Santana et al. 2013); (Rakotonirina et al. 2017)
Reptiles & Amphibians	Auditory	**Social structure** - Intensity of male-male competition	**Uncertainty – gradation** - Call amplitude modulation - Call duration	(Ord and Garcia-Porta 2012)
	Visual	**Social structure** - Intensity of male-male competition	**Number of signaling units** - Number of ornaments - Number of head bobbing **Uncertainty – gradation** - Duration of display	(Ord and Garcia-Porta 2012)

However, despite this imbalance in previous studies of different modalities and the diversity of methods used to assess communicative complexity across these modalities, some commonalities exist (Table I.1). According to the most common definitions, communicative complexity can be quantified via two main approaches: the number of distinct signals or signaling units or the number of bits of information included in signals (Griebel and Oller 2008; Pollard and Blumstein 2012; Freeberg et al. 2012a). In the following, we summarize how these two approaches have been applied across the three main modalities studied in the context of the SCHCC and identify their current limitations. At the end of this section, we argue in favor of enhanced acknowledgement of the multimodal aspect of communication within the framework of the SCHCC.

a. Number of distinct signals or signaling units

In all communicative modalities, the number of distinct signals or signaling units has been used as a proxy for communicative complexity. To assess vocal communicative complexity across species, vocal repertoire size, defined as the number of call type individuals of a population or species produce, has been mainly used. To this end, call types have been classified by visual inspections of spectrograms, a rather subjective approach. Although the more recently used quantitative approaches to estimate repertoire size are favored, subjectivity still persists in the way algorithms are implemented to classify call types (Fischer et al. 2017b). This bias, together with the diversity of quantitative methods applied to identify call types, currently results in substantial inhomogeneity among studies. For example, the vocal repertoire of the Mongoose lemur (*Eulemur mongoz*) has been characterized by visual inspection as composed of either 8 (Petter and Charles-Dominique 1979), 10 (Curtis and Zaramody 1999), or 14 (Gamba et al. 2015) call types, whereas quantitative analyses suggested 9 (Gamba et al. 2015) or 15 (Nadhurou et al. 2015) different call types. Thus, there is currently no general agreement on how to identify different call types and, hence, how to assess vocal repertoire size objectively.

Similarly, the main variable used to access complexity in olfactory signaling is the number of distinct chemical compounds contained in the different excretions (guinea pigs: (Beruter et al. 1973); primates: (delBarco-Trillo et al. 2011, 2012); hymenoptera: (Kather and Martin 2015). While some semiochemicals are composed of only one molecule (e.g., the female sex pheromone (Z)-7-dodecen-l-yl-acetate common to the Asian elephant (*Elephas maximus*) and several species of moths; (Wyatt 2003), others are composed of a combination of several molecules. Moreover, the diversity of scent sources, as urine, feces, saliva, skin secretions, or specialized sent glands, has also been considered as a proxy to assess olfactory complexity (delBarco-Trillo et al. 2011; delBarco-Trillo and Drea 2014). In addition, olfactory communication is characterized by its temporal duality: while scent deposition is a one-off event, the scent itself usually persists for some time and can be perceived by receivers even after the departure of the sender. Because scent deposition is usually accompanied by a typical behavior, we propose that the number of scent-marking behaviors can also be used to characterize the complexity of an olfactory system, even though these behaviors often have a strong visual component. Although repertoires of scent-marking behaviors have been reported for some species, they have rarely been interpreted in the context of the SCHCC (Drea and Scordato 2008; Colquhoun 2011; delBarco-Trillo et al. 2011).

Regarding visual signals, the numbers of both static and visual signals have been used as a proxy for complexity, although only a few studies actually tested the SCHCC. For example, among 25 wasp species, flexibly nesting species (with either one or several foundresses) exhibited more intraspecific variation in body markings than species having a unique nesting strategy (Tibbetts 2004); Table I.S1). In addition, dynamic signals, such as the number of visually distinct facial movements correlate with group size in Old World primates (Dobson 2009); Table I.S1).

To summarize, the number of signals or signaling units is a widespread method of accounting for complexity across modalities (Table I.1). However, this section also emphasizes the diversity of levels that may be evaluated through this approach. While some of these approaches may be applied at the system level across modalities (e.g., number of signaling behaviors), some others are more modality-specific and are usually applicable at the signal level (e.g., number of compounds, number of notes).

b. Number of bits of information or amount of uncertainty

This approach is based on information theory and represents a measure of the entropy of a system, which is an estimate of the amount of uncertainty (Cuthill et al. 2017; Fischer et al. 2017b). Thus, Shannon's entropy is not a measure of what one communicates, but rather a measure of what one could communicate (Shannon and Weaver 1949; Robinson 2008). This is an essential conceptual difference that may help to avoid circularity. Indeed, considering the social information contained in signals, rather than the possibilities offered by the structure of these signals to convey flexible and diverse information as a measure of communicative complexity, may lead to non-informative tests of the SCHCC. From a fixed set of signals, more information may first emerge by combinations, either through assemblage (simultaneous expression of different signals) or sequence (succession of different signals). Hence, acoustic units, i.e., uninterrupted traces in a spectrographic representation, and discrete calls can be combined into sequences (Bouchet et al. 2013; Manser et al. 2014).

Vocal sequences have been an intense area of research in studies of birdsong (Kroodsma 2004; Catchpole and Slater 2008), but the existence of non-random vocal structures has also been shown in several mammalian orders, including cetaceans (Riesch et al. 2008; Shapiro et al. 2011; Cholewiak et al. 2013; Zwamborn and Whitehead 2017), primates (Clarke et al. 2006; Arnold and Zuberbühler 2008; Zuberbühler and Lemasson 2014; Gustison et al. 2016), bats (Kanwal et al. 1994; Bohn et al. 2009) and hyraxes (Kershenbaum et al. 2012). The combination of signals is an alternative way to increase the amount of information transmitted, and several methods have been proposed to analyze the structure and rhythmicity of these sequences (reviewed in (Kershenbaum et al. 2016; Ravignani and Norton 2017). Indeed, the number of call/note combinations correlates with group size in several species (Freeberg 2006; Bouchet et al. 2013; Manser et al. 2014), suggesting that this is a promising area for future research on communicative complexity.

Similarly to vocalizations, olfactory signals can also be produced in sequences and the combinational deposition of scents appears to be widespread in mammals (Mills et al. 1980; Vogt et al. 2014; Clapham et al. 2014). For instance, male ring-tailed lemurs (*Lemur catta*) flexibly use two specific scent glands, by either depositing only one type of scent or a mixture of the two secretions. The mixture elicited a higher responsiveness, suggesting that they contain a larger number of messages and persist for longer (Greene et al. 2016). The superposition or juxtaposition of different scent-marks may also be studied following the same analytical methods as the ones mentioned above for acoustic sequences (Kappeler 1998). Similarly, numerous courtship displays have been described as assemblages or sequences of different visual signals (Lorenz 1941), but these combinations have rarely been related to sociality in a comparative perspective (Crook 1964).

Variability in the structure of signals presents another potential way to increase the amount of transmitted information. For example, vocal systems have been suggested to be either discrete, with acoustically distinct call types that are easily discriminated from each other, or graded, with the acoustic structure of the vocalizations forming a continuum without clear boundaries between different call types (Marler 1977a; Keenan et al. 2013). The gradation level is a measure of the overlap in temporal and spectral features existing between two calls, and might be one of the main reasons for the inconsistency in measures of vocal repertoire sizes. The higher the level of gradation in a system, the more difficult it is to cluster its components, but the higher is the potential for information transmission. Gradation may therefore represent a measure of bits of information that may be contained in signals. Because vocal repertoires usually contain a combination of discrete and graded calls (Fichtel et al. 2001; Bouchet et al. 2013; Manser et al. 2014; Fischer et al. 2017b), the level of gradation can also be used to operationalize the complexity of a vocal system (Fischer et al. 2017b).

Different selective pressures seem to shape signals as a function of the quantity of information required from a signal. While stereotypical signals with high context specificity reduce ambiguity, more flexible signals can convey more subtle and complex information about the sender's motivational state or a particular context (Fischer 1998; Fichtel et al. 2001; Griebel and Oller 2008; Manser et al. 2014). Accordingly, the "call social function hypothesis" proposes that the level of overlap in temporal and spectral features of a call type will be influenced by its social function (Snowdon et al. 1997; Griebel and Oller 2008; Lemasson and Hausberger 2011; Bouchet et al. 2013; Keenan et al. 2013). In female Campbell's monkeys (*Cercopithecus campbelli*), calls associated with the highest affiliative social value exhibited the greatest gradation level, whereas calls associated with agonism were the most stereotyped, and less social alarm calls were of intermediate variability (Lemasson and Hausberger 2011; Table I.S1).

Furthermore, inter-individual variation in call structure is another source of gradation that might be impacted by group size. The more group members interact, the more they may benefit from accurately recognizing the sender of a call, but this recognition task becomes increasingly difficult with increasing group size (Freeberg 2006; Pollard and Blumstein 2011). Hence, if individual recognition is important, more individualistic signatures should evolve with increasing group size as shown, for example, in chick begging calls of swallows (cliff swallows *Hirundo pyrrhonota* and barn swallows *Hirundo rustica*; (Medvin et al. 1993), alarm calls of ground-dwelling sciurids (Pollard and Blumstein 2011), and infant isolation calls of bats (Wilkinson 2003; Table I.S1).

Hence, the gradation level of the vocal system (1 in Figure I.2), the gradation level of different call categories (2 in Figure I.2), and the stereotypy of different call types (3 in Figure I.2), as well as the level of individuality in different call types (4 in Figure I.2), are all sources of gradation that may be impacted by social variables. However, a practical quantitative measure is still lacking to evaluate gradation at the system level. The distribution of call stereotypy coefficients has recently been suggested as a potential measure of gradation for comparative analyses, with right-skewed distributions (closer to 1) indicating higher differentiation and left-skewed distributions (closer to 0) indicating a higher degree of gradation (Wadewitz et al. 2015; Fischer et al. 2017b). By applying a fuzzy-c-means cluster algorithm, which allows for imperfect membership, calls can be assigned to different clusters. For each call a membership value is attributed for each cluster, ranging from 1 (the call fully displays the properties of the cluster in question) to 0 (the call does not display any of the properties of the cluster). The call stereotypy coefficient (referred to as "typicality coefficient" in Wadewitz et al. 2015 and Fischer et al. 2017b) can then be obtained by subtracting the two highest membership values associated with this call. Hence, this measure allows for quantifying the gradation level between two call types but does not provide a generic measure of the gradation level of the vocal repertoire. Therefore, we suggest that the distribution of the standard deviations across membership values for each call might be a more appropriate measure of gradation at the system level.

Although this approach to assess the gradation level between signals has almost exclusively been adopted in the acoustic modality, the level of overlap in signal features may theoretically also be applied to other modalities. Hence, the relative proportions of different chemical components may also be considered as a form of gradation, with possible variation among species, groups, and individuals (Symonds and Elgar 2008; delBarco-Trillo et al. 2011). This gradation approach has also been suggested to be applicable to dynamic visual signals, such as facial expressions and gestures (Fischer et al. 2017b), but this remains to be explored in practice.

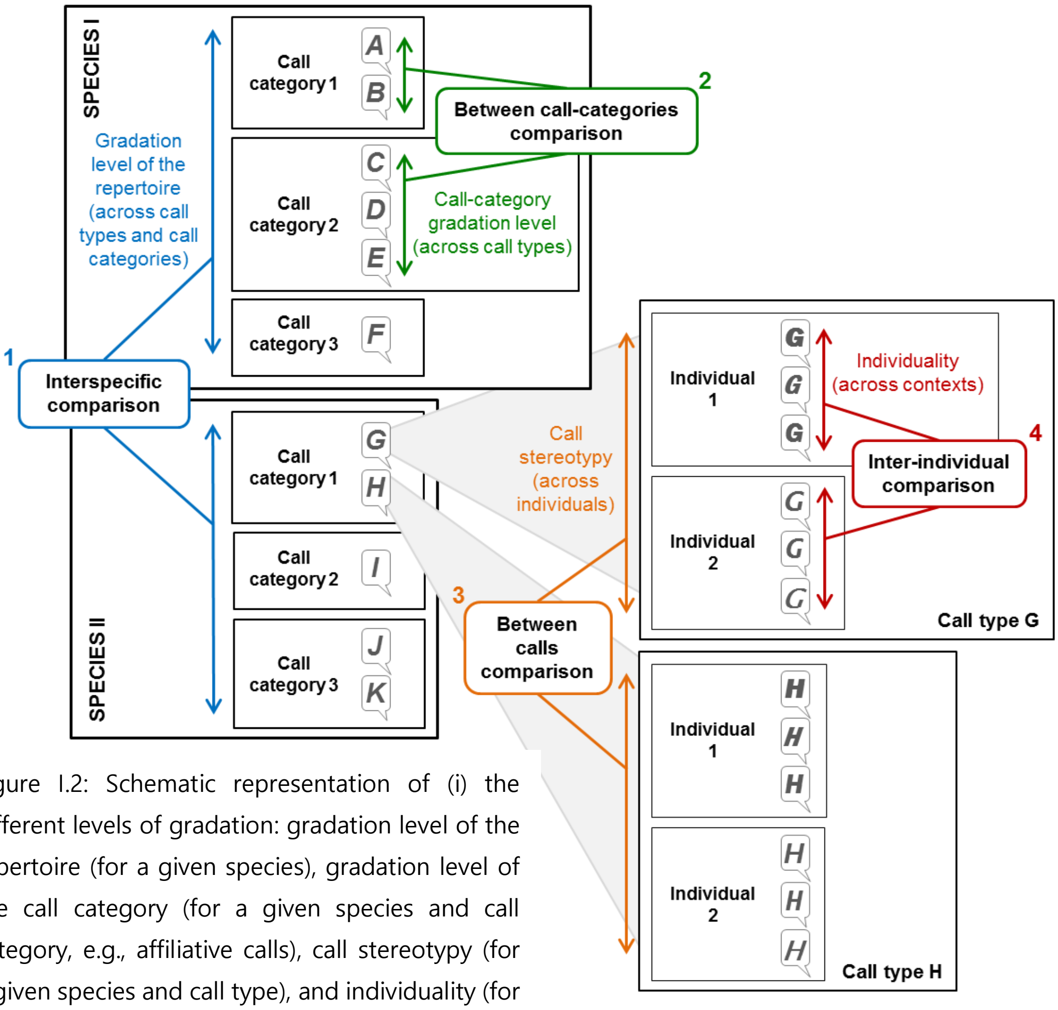


Figure I.2: Schematic representation of (i) the different levels of gradation: gradation level of the repertoire (for a given species), gradation level of the call category (for a given species and call category, e.g., affiliative calls), call stereotypy (for a given species and call type), and individuality (for a given call and a given individual) and (ii) the associated potential comparative levels (1 to 4). Each gray capital letter represents a different call type, e.g., A is a call type of category 1 produced by the individuals of species I

A final approach to assess communicative complexity is to evaluate the perceptive adaptations of a system. This approach is highly complementary with the precedent one as in all species, sensory capabilities co-evolved with the range of signals they produce. Moreover, it should provide information on the ability of the receiver to discriminate between different stimuli. Hence, from an evolutionary point of view, this approach is significant, but has only rarely been addressed (Ramsier et al. 2012; Elgar 2015). For example, foraging group size co-varied with the overall hearing sensitivity and high-frequency limits across 11 species of strepsirrhine primates, suggesting that social complexity favored enhanced hearing sensitivities, especially at higher frequencies (Ramsier et al. 2012; Table I.S1). Similarly, in the olfactory domain, social Hymenoptera species have higher densities of hair-like sensillae, with which they perceive olfactory signals, compared to species that became solitary (Wittwer et al. 2017; Table I.S1). Comparative studies on visual adaptations may also be informative (Endler et al. 2005), but studies of variation in visual communication have so far mostly considered effects of ecological factors, such as background vegetation (Fleishman 1992), habitat type (Malacarne et al. 1991), or diurnality and predatory habits (Veilleux and Kirk 2014).

To summarize, evaluating the amount of uncertainty in a signal or signaling system represents a common approach to evaluate communicative complexity across modalities (Table I.1). Although the most common approach is to study of combinational use of signals, the concept of gradation, currently mainly used for the vocal modality, is a really promising one that may allow for a systematic evaluation of communicative of complexity at both the signal and system level. This approach may benefit by also considering the complexity of the associated perceptive adaptations.

Thus, across all three modalities discussed here, several complementary approaches of complexity appear particularly relevant. These approaches are based on the number of signals or signaling units and the uncertainty (combinations and gradation of signals). These approaches are applicable across modalities and address both signal and system levels and may therefore also be used for broad comparative studies. As for measures of social complexity, we encourage the development of complementary quantitative operational measures of communicative complexity that incorporate the insights addressed above.

c. *Integrating the multimodal nature of communication*

While the field of animal communication has moved in the early 2000s from a unimodal approach to a multimodal one, acknowledging the fact that most animals produce signals across different modalities (Mcgurk and Macdonald 1976; Partan and Marler 1999; Rowe 1999; Candolin 2003; Hebets and Papaj 2005), much research in the context of the SCHCC has remained focused on a single modality. However, there are several good reasons for acknowledging the multimodal nature of signals and communicative systems in this framework. Two fundamental aspects of communication effectively deserve some attention, first, at the signal level, the fact that numerous signals are by themselves multimodal and, second, at the system level, the fact that individuals, even when not using multimodal signals, usually communicate through different modalities (Liebal et al. 2013; Pika 2017).

Multimodal signals are by definition complex, because they involve more than one signaling and perceptive system (Rowe 1999; Smith and Evans 2013). Moreover, multimodal signals have been suggested to be widespread in group-living animals (Partan and Marler 1999), but this assumption has never been formally tested. Isolating one component of a multimodal signal may lead to false conclusions because some signals have a different function when they are expressed independently or together with another signal component ("multiple signals/messages hypothesis" and "disambiguation hypothesis"; (Hebets and Papaj 2005; Liebal et al. 2013). For example, female red-winged blackbirds (*Agelaius phoeniceus*) use the same visual display for courtship and aggression, and only the addition of a vocalization allows discrimination between contexts (Beletsky 1983).

At the system level, focusing on one modality only may lead to over- or underestimation of the relationship between social and communicative complexity, respectively. For example, submission in primates can be expressed either by visual or acoustic signals (Jolly 1966a; de Waal and Luttrell 1985), showing that the same social selective pressure may result in different signaling adaptations that are equally complex but expressed through different modalities. Second, the flexible use of different modalities in multimodal signals permits another level of complexity embedded in multimodal signaling (Liebal et al. 2013; Wilke et al. 2017). For example, captive chimpanzees (*Pan troglodytes*) used more tactile and vocal signals when the experimenter was facing away, but more visual-gestural signals when the experimenter was facing the chimpanzee (Leavens et al. 2010). Thus, depending on the species in question, it may also be highly relevant to include some modalities (e.g., vibratory, thermal, electrical) that are not addressed here because they have not yet been considered in the framework of the SCHCC.

Hence, we suggest that establishing a cross-modal signal repertoire would not only fill the gap in our current understanding of the multimodal nature of most signals (Partan and Marler 2005) and contribute to a more comprehensive assessment of communicative complexity, but would also allow more meaningful tests of the SCHCC (Liebal et al. 2013; Waller et al. 2013). Moreover, applying a multimodal approach may also help to uncover the different selective pressures acting on the communicative system and to better understand adaptive functions that might not be clear from the study of its components independently (Liebal et al. 2013).

3. Integration of expanded operational definitions

We argue that integrating appropriate quantitative measures of social complexity (as described above) together with cross-modal measures of communicative complexity (number of signaling units and uncertainty) in a holistic fashion should facilitate comparative research on the SCHCC and may reveal important avenues for future research. Although the development of appropriate analytical tools to study multimodal communication has been debated for a while (Partan 2013), a recent network approach has offered great promise. This method has been used to uncover the contributions of female mate choice and male-male competition in the North American barn swallows (*Hirundo rusticaerythrogaster*) via examining a comprehensive array of phenotypic variables by a correlation-based phenotype network (Wilkins et al. 2015; Hebets et al. 2016). A similar approach could be used for a systematic analysis of communication systems and their links with social parameters. For example, each node in a signal phenotype network may represent a different signal/signaling unit or a different communicative complexity measure, with different node shapes representing different modalities or types of signals. The edge between two signals may then represent the correlation between these two signals across individuals in terms of either frequency of occurrence (Example 1 in Figure I.3) or value (Example 2 in Figure I.3) or their temporal association (Example 3 in Figure I.3), depending on the chosen measures. The comparison of these communicative system representations across different social context (e.g., activities or audiences) may, for instance, reveal new interesting relationships between communicative signals and social parameters. Integrating relevant social parameters into these networks would also allow exploring the specific links between different social and communication variables at the system level (Wilkins et al. 2015). The application of such a system-inspired framework, for example, revealed dynamic changes in signal structure and function across environmental and social contexts in courtship displays of wolf spiders (*Schizocosa floridana*) (Rosenthal et al. 2018).

Hence, we believe that this method would not only offer instructive visual representations of multimodal communicative systems, but also an opportunity to extract new quantitative and broadly applicable measures that could be interpreted in terms of communicative complexity. This method indeed offers the possibility to characterize a given system in terms of degeneracy, modularity and pluripotentiality (Wilkins et al. 2015; Hebets et al. 2016). Degeneracy is a measure of network density and represents the number of significant correlative relationships; a highly degenerated system will be composed of signals potentially carrying the same information or having the same function (see “redundancy” in (Wilkins et al. 2015); Examples 1 and 2 in Figure I.3). Modularity represents the degree to which relationships exist across versus within clusters, here representing signal types or modalities; a highly modular system will be composed of more modality-specialized individuals (Wilkins et al. 2015); Example 2 in Figure I.3). Pluripotentiality is a measure of the degree to which identical display components function across contexts; a highly pluripotent system will be composed of more functionally flexible signals that are used across contexts (Hebets et al. 2016).

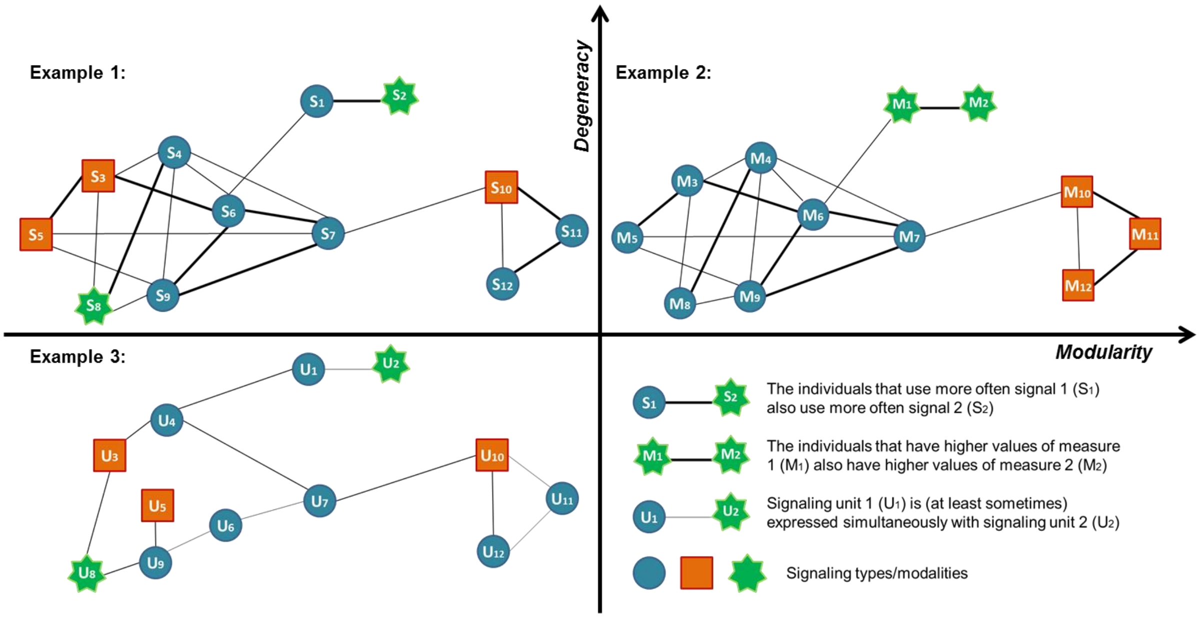


Figure I.3: Three heuristic examples of possible network construction presented on a conceptual diagram showing different levels of system degeneracy and modularity. The meaning of the edge and nodes for each example are explained in the bottom-right quarter. This figure is adapted from (Wilkins et al. 2015)

Hence, in the context of the SCHCC, we make a plea for more comprehensive study of communicative systems, integrating a set of quantitative and complementary measures of social and communicative complexity and accounting for the multimodal aspect of communication. We believe that his approach would bring considerable insights in the current debate, particularly allowing for the emergence of more specific predictions on the nature of the link between social and communicative factors.

III. The links between social and communicative complexity

Although several studies have supported the social complexity hypothesis by revealing correlative relationships between social and communicative variables, only a few studies have examined and discussed the nature of these links in detail. Hence, the direction of causality and the mechanisms underlying these links remain currently unclear (Freeberg et al. 2012a; Ord and Garcia-Porta 2012; Gustison et al. 2016, 2019), and these questions would benefit from additional research.

1. Control for alternative hypotheses: directionality and strength of the links

When studying the SCHCC, it is essential to also consider potential alternative hypotheses driving the evolution of signals. This is fundamental in both situations when a correlational link is found or when no such link is found, even though a link would be predicted (Freeberg et al. 2012a). For both outcomes, several alternative explanations are possible (Figure I.4), revealing two fundamental problems. First, the relative role of social complexity in shaping communicative complexity needs to be assessed. Social complexity may shape the complexity of a particular set of signals synergistically with other selective pressures also selecting for more complexity (Figure I.4, scenarios A and B) or despite other additional selective pressures (selective forces act in opposite directions; Figure I.4, scenarios C and D), making it hard to extract the actual effect of social complexity itself (Figure I.4, scenarios B and D).

Second, correlative studies do not permit conclusions about the direction of causality. Complex communicative systems may evolve in response to pressures related to social complexity, but complex communicative systems might also be driven by other selective pressures independent of changes in sociality that could in turn facilitate the evolution of greater social complexity (Figure I.4, scenario E; (McComb and Reby 2005; Freeberg et al. 2012a; Ord and Garcia-Porta 2012). For example, a comparison across 22 species of lizards revealed that the number of head-bobbings was better explained by habitat use, i.e., the level of arboreality, than by the intensity of competition among males (Ord and Garcia-Porta 2012). Similarly, a comparison across 23 species of birds revealed that syllable repertoire size was better explained by body size than by the level of extra-pair paternity, and a comparison across 32 species of frogs revealed that the level of call amplitude modulation was better explained by phylogeny than by the intensity of competition among males (Ord and Garcia-Porta 2012).

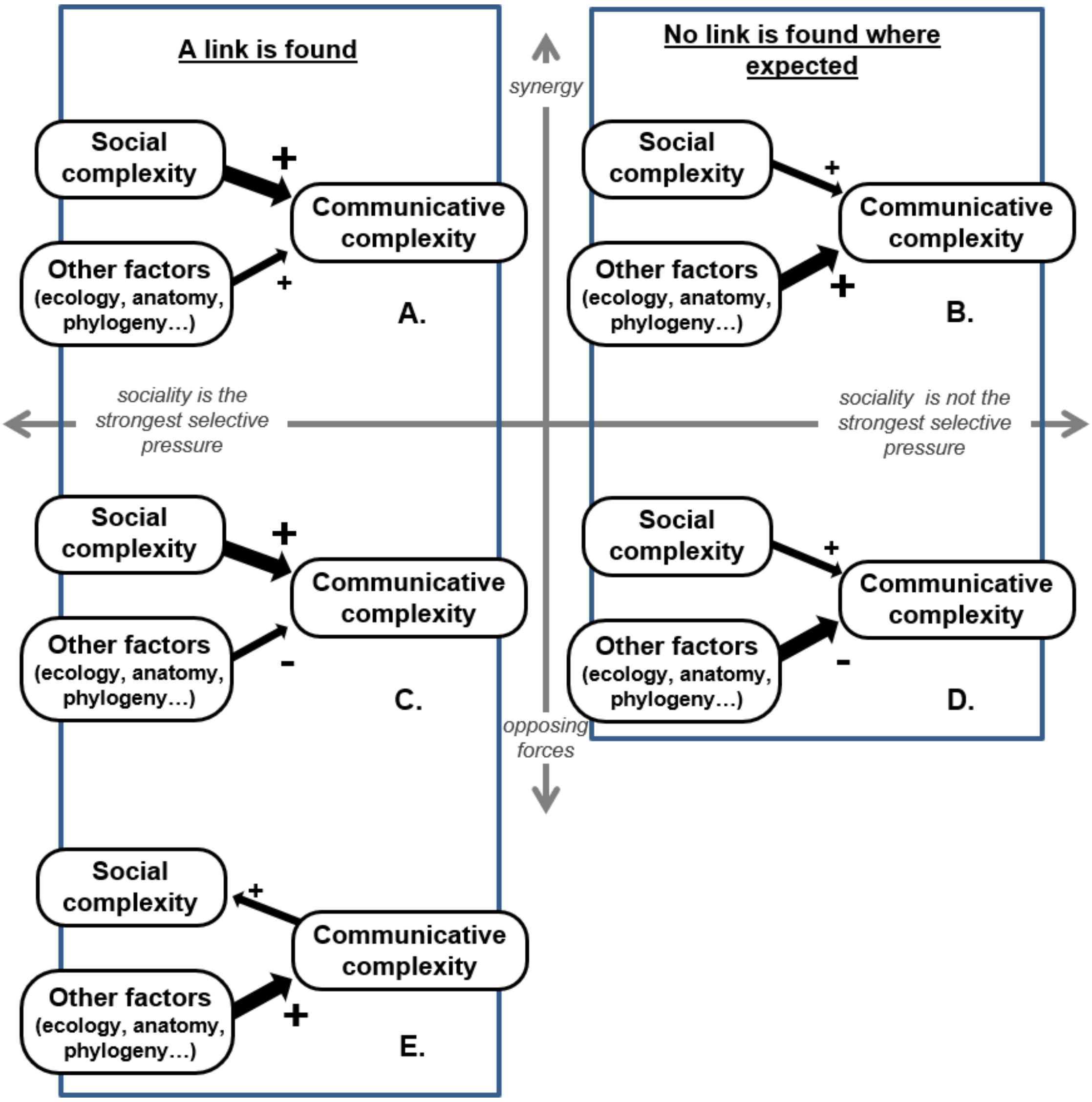


Figure I.4: Schematic representation of different potential evolutionary scenarios depicting the link between social and communicative complexity. A: scenario in which a link is observed, social complexity is the main selective pressure driving communicative complexity, in parallel other factors also contribute selecting for communicative complexity; B: scenario in which no link is observed with social complexity because other selective pressures have a stronger effect on the evolution of communicative complexity; C: scenario in which a link is observed, social complexity is the main selective pressure driving communicative complexity even if other factors constrain the evolution of communicative complexity; D: scenario in which no link is observed with social complexity because the effect is counterbalanced by other selective pressures constraining the evolution of communicative complexity; E: scenario in which a link is observed but communicative complexity is under other selective pressures and drive itself the evolution of more complex social systems

Hence, non-social selective pressures such as ecology, anatomy or a phylogenetic null model explained changes in signaling complexity better than the specific aspects of social complexity considered in these analyses (Ord and Garcia-Porta 2012); Figure I.4, scenario B). The mechanisms underlying these selective pressures have been explicated by Freeberg et al. (Freeberg et al. 2012a) and are summarized in Table I.2. In general, the evolution of complex signaling systems is presumably not the result of a single specific selective pressure but rather the result of a combination of several ones (Freeberg et al. 2012a; Ord and Garcia-Porta 2012; Ramsier et al. 2012; Manser et al. 2014). Thus, if two species have similar social systems but only one experiences a specific ecological challenge, different types of signals may evolve, but these signals will not necessarily differ in complexity. And, as argued above, the same selective pressure may lead to different adaptations that may be equivalent in terms of complexity but involve different modalities.

To deal with these complications, appropriate statistical tools controlling for alternative hypotheses are required. For example, phylogenetic comparative studies can reveal the order in which different traits evolved in a given lineage (e.g., Podos 2001; Wittwer et al. 2017). Model fitting procedures may also allow for assessing the relative role of the different factors in selecting for communicative complexity and test the SCHCC against alternative hypotheses (Ord and Garcia-Porta 2012). Control of the alternative hypotheses may also be achieved by a quasi-experimental approach that includes the study of closely related species sharing similar habitats, climatic conditions, food resources, parasites, and predators, but exhibiting differences in their social systems (Krams et al. 2012; Ord and Garcia-Porta 2012).

Table I.2: Summary of the mechanisms underlying alternative hypotheses for the evolution of communicative complexity. This table is inspired by (Freeberg et al. 2012a)

Factor		Signal complexification	Signal simplification
Ecology	**Habitat**	▪ **Addition of an alert element** e.g., yellow-chinned anoles (*Anolis gundlachi*) add an alert signal to their visual displays in situations of poor visibility (Ord and Stamps 2008) ▪ **Combinations of long distance and close distance components** e.g., the white-browed warbler *Basileuterus leucoblepharus* combined long or short-range transmission of information in a single song (Mathevon et al. 2008) ▪ **Multimodal signals** e.g., Male wolf spiders (*Schizocosa ocreata*) combined long or short-range transmission of information by combining vibratory and visual courtship signals (Uetz et al. 2009)	▪ **Alert components generally have simple structure**
	Predation	▪ **Evolution of alarm calls** e.g., Campbell's monkeys (*Cercopithecus campbelli*) concatenate vocalizations into predator-specific call sequences (Ouattara et al. 2009) ▪ **Pursuit-deterrent signals to signal condition** e.g., tail-wagging behavior of the zebra-tailed lizard (*Callisaurus draconoides*) (Hasson et al. 1989)	▪ **Use of basic calls to avoid attracting predators** e.g., When the probability of predation is high, males Tungara frogs (*Physalaemuspustulosus*) compromise on signal complexity and produce only the most basic call (Ryan et al. 1982)
	Sympatry	▪ **Less overlap probability between signals if more complex** e.g., Neotropical primates species living in sympatry with a higher number of congener species have evolved more complex patterns of facial color (Santana et al. 2012)	
Phylogeny	**Neutral evolutionary processes**	▪ **Genetic drift may lead to more complex signals** e.g., facial color complexity in lemurs (Rakotonirina et al. 2017)	
Morphology			▪ **May constrain abilities and impose tradeoff** e.g., wood warblers (*Parulidae*) show a tradeoff between trill performance (syllable repetition) and song complexity (syllable diversity) (Cardoso and Hu 2011)

2. Identification of the underlying mechanisms: exploring the relationship(s) between signal variation and social factors

How variation in signaling is directly affected by social factors is usually not explored, failing to uncover both the specific attributes of communication that would evolve in response to specific aspects of sociality and the actual way these social factors may influence signaling behavior (Pollard and Blumstein 2012; Gustison et al. 2012, 2019). In the next sections, we offer suggestions on how to explore the nature of these relationships with both, ultimate (e.g., function of derived calls or complex signals) and proximate approaches (e.g., audience effect and social learning).

a. Studying the social function of derived signals

One approach to begin closing this gap is to study the social function of derived signals to obtain a better understanding of the functional meaning of the observed differences (e.g., why a larger vocal repertoire evolved in the more socially complex species). Identifying the relevant differences (e.g., which are the derived calls?), their social functions (e.g., what are the social functions of these derived calls?) and assessing potential fitness consequences of these derived signals in detail will help to identify the potential social selective factors driving the evolution of these signals (Gustison et al. 2012; Liebal et al. 2013).

Regarding the vocal modality, it has been shown that rather than an overall increase in repertoire size, an increased number of different calls are generally found only in one or two call categories, with species exhibiting greater social complexity having vocal repertoires including a greater proportion of vocalizations used in affiliative contexts (Le Roux et al. 2009; Taylor and Reby 2010; Fedurek and Slocombe 2011; Briefer 2012; Gustison et al. 2012). A descriptive identification of derived call categories has been conducted in a relatively small set of closely related species (Kroodsma 1977; Stirling and Thomas 2003; Manser et al. 2014), but recently also in a comparative study across 253 bird species (Leighton 2017; Table I.S1). Birds breeding cooperatively had a significantly larger vocal repertoire size than other species. This increase in repertoire size was due to specific increases in the number of alarm and contact calls but not aggression, flight, territorial, or mating calls. Although this contextual information is undeniably valuable for discussing the SCHCC, these broad categories nevertheless fail to uncover the specific social function at stake.

In contrast, a detailed comparison of the vocal repertoire of two closely related primate species (chacma baboons, *Papio ursinus*, and geladas, *Theropithecus gelada*) with different social systems, identified eight homologous calls, but also six derived calls present only in the geladas, suggesting that the socially more complex geladas have larger vocal repertoires (Gustison et al. 2012; Table I.S1). Gelada males use these calls to maintain social relationships with females in their units and specifically direct these calls towards females after conflicts. Interestingly, this difference parallels a social divergence between the two species because gelada males form long-term bonds with several females in a harem-like reproductive unit, whereas chacma males only form temporary associations with females. Hence, comparing the nature of the difference between signal repertoire sizes between species that differ in aspects of their sociality can help to uncover the role of the respective social factors in explaining the observed variation between the communicative systems.

b. Audience effects and signal complexity

The audience effect is defined as a change in signaling behavior caused by the presence of the audience; the audience being defined as any individual that is within the signal range (Marler et al. 1986; McGregor and Dabelsteen 1996). Therefore, signaling behaviors may be influenced not only by the characteristics of a targeted receiver (Fröhlich et al. 2016) or its attentional state (Leavens et al. 2010; Smith et al. 2011) but also by the nature of the audience (Slocombe and Zuberbuhler 2007; Kalan and Boesch 2015; Crockford et al. 2017) including unwanted receivers (Matos and McGregor 2002; Smith et al. 2011). Hence, the SCHCC could provide a theoretical framework for testing audience effects by considering variation in the audience as an aspect of social complexity. Studying audience effects on complex signals may therefore help to uncover the particular social selective pressures that may have led to the evolution of flexible signals. Multimodal or multicomponent signals appear to be particularly good candidates to examine this audience effect.

First, signals including functionally redundant components may serve to increase signal detection and memorization ("backup hypothesis": Johnstone 1997; "receiver psychology hypothesis": Rowe 1999). This type of signal may optimize signal transmission but may also attract the attention of unwanted receivers. Hence, to balance benefits and costs, multicomponent signals should be associated with some behavioral flexibility, allowing variation in usage and signal structure (e.g., only one component is expressed) between contexts (e.g., more discrete signal when unwanted receivers are in proximity). Male jungle fowl (*Gallus gallus*), for example, exhibit variability in their tidbitting food-call recruitment behavior used not only to attract females but also to trigger aggression of male competitors (Smith et al. 2011). Tidbitting is a visual signal consisting of repetitive movements of the head and neck and can be combined with repetitive pulsatile sounds. Subordinate males adapt this display to the attentional state of the alpha male of the group by producing more frequently bimodal tidbitting when the alpha male is distracted (Smith et al. 2011).

Second, signals including non-functionally redundant components may carry additional information ("multiple messages hypothesis": (Moller and Pomiankowski 1993) that might be addressed at different audiences and may also be flexibly adapted between contexts. Even if it remains to be tested, this may be particularly true for mammal scent-marking behaviors ("demonstrative marking hypothesis"; Estes 1967; Johnston 2005) because of its temporal duality. Scent deposition behaviors often include obvious visual signals that may reach individuals present in the vicinity of the sender, while the scent itself may be directed towards both the present and future audiences.

Hence, studying the flexibility of complex signal usage (e.g., occurrence or structural modifications) across social contexts (audiences) will permit to identify the different individual social characteristics that may elicit or constrain complex signal expression. These social characteristics may later constitute social pressures acting for or against the evolution of these complex signaling behaviors.

c. *Ontogeny of flexible signaling behavior: social contexts associated with vocal production learning flexibility in vertebrates*

Despite fundamental similarities in the structure and mechanisms of vocal production systems across vertebrates, important differences exist between species at the level of flexibility in vocal production. Accordingly, a distinction is usually made between vocal learners and non-vocal learners. Non-vocal learner species produce adult-like vocalizations from birth onward and usually possess a relatively small vocal repertoire, which is genetically controlled and evolutionarily conserved. In contrast, vocal learner species learn their vocalizations from another conspecific (social tutor). Early vocalizations are usually structurally simple and highly variable, becoming more complex and stereotyped with age. In some species, vocal learning occurs only during a specific early sensitive period, whereas others exhibit open-ended vocal learning (Egnor and Hauser 2004; Catchpole and Slater 2008).

In contrast to vocal contextual learning (in which “a pre-existing signal comes to be associated with a new context”, (Janik and Slater 2000), vocal production learning refers more specifically to the modification in the structure of vocal signals through experience with another conspecific (Janik and Slater 2000; Ruch et al. 2018). These changes in vocalizations can be classified as either vocal accommodation, when existing vocalizations are modified, or lexical learning, when a new vocalization is acquired (Ruch et al. 2018). The latter form of vocal learning is particularly interesting in the context of the SCHCC as it may lead to an increasing number of signals used by an individual across its lifespan. So far, evidence for lexical learning was only found in three distantly related groups of birds (parrots, hummingbirds, and songbirds) and four distantly related groups of mammals, i.e., humans (but not in other primates), bats, cetaceans, and elephants (Nowicki and Searcy 2014; Ruch et al. 2018).

In most of these species, individuals exhibit babbling-like behavior in early life (bats: (Knörnschild et al. 2006); cetaceans: (Vergara and Barrett-Lennard 2008); parrots: (Masin et al. 2004). Babbling not only is primarily considered as an essential practice for vocal learning but also seems to play a key role in social exchanges with caregivers (Vergara and Barrett-Lennard 2008; Tallerman and Gibson 2012). In humans, babbling triggers positive responses from kin as well as non-kin caretakers (Tallerman and Gibson 2012). Hence, babbling should be particularly adaptive in species displaying allomaternal care, as for example in cooperative breeders. In this social environment, young have to compete with each other for the attention of non-kin helpers. Interestingly, allomaternal care is present in all the families mentioned above exhibiting lexical learning (cetaceans: (Hill and Campbell 2014); humans: (Tallerman and Gibson 2012); elephants: (Rapaport and Haight 1987); birds: (Hatchwell 2009). For example, humans and callitrichids exhibit the greatest degree of allomaternal care among primates, and they are the only primate taxa with babbling infants (Tecot et al. 2012; Burkart et al. 2017). This potential link between the presence of allomaternal care and lexical learning is also consistent with the relatively recent idea of a possible co-evolution between vocal communication complexity and cooperation (Tallerman and Gibson 2012; Freeberg and Krams 2015). Hence, more elaborate vocal behavior and babbling-like behavior might be more common in species with allomaternal care. The examples illustrate the point that studying the social environments in which flexible vocal learning takes place may also illuminate the causal relationships between social variables and communicative complexity.

IV. Conclusions

Many previous studies of communicative complexity have focused on specific links between single social and communicative variables, oversimplifying the complexity of these interrelations and ignoring the specific underlying mechanisms. We therefore make a plea for more specific predictions and a more comprehensive study of communicative systems. We particularly recommend:

(1.) To apply broadly applicable quantitative measures of social complexity in order to avoid the pitfalls of subjectivity and circularity and to clarify the level at which complexity is evaluated.

(2.) To assess communicative complexity at the system (repertoire) level, accounting for the multimodal nature of communication at both the signal and system levels.

(3.) To control for alternative hypotheses to the SCHCC through the application of appropriate statistical methods or careful selection of study species.

(4.) To develop more specific predictions about particular social factors that may impact a specific communication variable and the underlying mechanisms at play.

Moreover, we argue that integrating appropriate social and communicative complexity measures and studying the social contexts promoting complex signal expression in more detail may advance our current understanding of the links between social and communicative complexity. Integrating quantitative measures of social complexity with cross-modal measures of communicative complexity should help to uncover the selective pressures acting on the communication system and may additionally provide an opportunity to extract new quantitative and broadly applicable measures of communicative complexity at the system level. Studies of the social contexts associated with complex signal expression at both the ultimate and proximate level may identify the specific attributes of communication that evolve in response to specific aspects of sociality.

In summary, we propose that expanding tests of the SCHCC in scope (systematic approach across modalities) and depth (characterization of the observed relationships) will significantly advance our understanding of the intricate links between animal sociality and communication. Studying the SCHCC along these lines may also inform current debates in the study of social cognition, where communication is rarely discussed, as well as in studies of language origins and evolution.

V. Supplementary material

Table I.S1 Summary of studies reporting presence of links between social complexity and communicative complexity. This table is inspired by a table published in Pollard and Blumstein (2012). Blue lines were added in this version compared to the published one.

		Taxa (order, genre, species)	Number of species included	Proxy for social complexity	Proxy for communicative complexity	Statistical method	Method for control of phylogeny	Other controlled parameters	Details	Reference
Auditory	**Birds**	Birds	253 (59 families)	Cooperative breeding (absence/presence)	Vocal repertoire size	Phylogenetic generalized least squares analysis	Generalized least square	Habitat (generalized least-squares)	Cooperative breeders have significantly larger repertoire sizes than species without cooperative breeding	(Leighton 2017)
		Cliff swallows (*Hirundo pyrrhonota*) and barn swallows (*H. rustica*)	2	Colony size	Individuality in chick begging calls	Descriptive	Closely related species	Ecology (quite similar ecology)	The species with larger nesting colony size also has a greater individual distinctiveness in chick begging calls	(Medvin et al. 1993)
		Gulls *Larus*	2	Collective breeding ("nursery" presence or absence)	Potential for individuality coding in adult contact calls	Descriptive	Closely related species	None	Mobile "nursery" behavior is associated with greater potential for individual distinctiveness in adult contact calls	(Mathevon et al. 2003)
		Passeriformes, Carolina chickadees	1 (30 groups)	Social group size	Diversity of notes and notes pairings (uncertainty index)	General linear model analysis of variance	/	Call context	Calls of individuals in larger groups had greater diversity of notes and notes pairing than calls of individuals in smaller groups	(Freeberg 2006)

Auditory	**Birds**	Wrens, *Troglodytidae*	9	Mating system Between-group competition	Vocal repertoire size	Descriptive	Closely related species	None	Polygynous mating systems and high individual encounter rates within dense wren populations are associated with large song repertoires	(Kroodsma 1977)
	Mammals	Microchiropteran bats	8	Colony size	Individuality in infant isolation calls	Least-squares regression analysis	Closely related species	Age (linked to forearm length)	Roosting colony size is positively correlated with distinctiveness in infant isolation calls	(Wilkinson 2003)
		Mongooses *Herpestidae*	5	Social organization, social group size	Vocal repertoire size, number of affiliative call types	Descriptive	Closely related species	Body size (similar)	The number of discrete call types, especially the ones used in affiliative contexts increases from the more solitary living mongoose species to the obligate social living species but not a linear increase with group size	(Manser et al. 2014)
		Whales	35	Social group size	Mean minimum tonal sound frequency	Regression	Independent contrasts	None	Group size is significantly correlated with the mean minimum tonal sound frequency	(May-Collado et al. 2007)
					Number of tonal sound inflection points (tonal sound modulation)	Tests of character state associations			Complex whistles (more inflection points) are positively associated with group living species and negatively with less social species	

Auditory	**Mammals**	Phocid seals	12	Mating system (serial monogamy, promiscuous, polygamous)	Repertoire size of adult males	One-way ANOVA Linear regression Pearson's correlation	Closely related species	Predation pressure (Pearson's correlation)	Polygamous species have a greater number of male underwater vocalizations	(Stirling and Thomas 2003)
				Female gregariousness		Pearson's correlation			Female gregariousness is negatively correlated with the number of male underwater vocalizations	
		Campbell's monkeys	1	Social affiliative value (context)	Potential for identity coding	Descriptive	/	None	The greatest acoustic variability, within and among individuals, were found in calls associated with the highest affiliative social value	(Lemasson and Hausberger 2011)
					Call coefficient of variation					
		Cercopithecus	3	Social systems (mating system, dominance, grouping pattern)	Call variability	Friedman test	Closely related species	Habitat (similar)	Red-capped mangabey (strong hierarchy + relatively frequent physical interactions + large multi-male multi-female groups) threat calls were significantly more variable than the ones of Campbell's monkeys (discrete hierarchy + rare physical interactions + medium-size harems)	(Bouchet et al. 2013)
					Call rate	Kruskal-Wallis test			Red-capped mangabey call at significantly higher rates than the Campbell's monkeys	

Auditory	**Mammals**	Cercopithecus	3	Social systems (mating system, dominance, grouping pattern)	Diversity index (complexity of the vocal repertoire in terms of "unit assembling pattern" types)	Descriptive			Female De Brazza's monkeys (discrete hierarchy + rare physical interactions + small family groups) displayed the less diverse repertoire and female red-capped mangabeys the most diverse repertoire	(Bouchet et al. 2013)
		Papio and Theropithecus monkeys	2	Social system	Repertoire size	Descriptive	Closely related species	None	The socially complex geladas have larger vocal repertoires	(Gustison et al. 2012)
		Primates	42	Social group size Grooming time	Adult vocal repertoire size	Multiple regression analysis	Independent contrasts	None	Contrasts in repertoire size are positively correlated with contrasts in group size and contrasts in time spent grooming	(McComb and Semple 2005)
		Primates	25	Dominance style (counter-aggression, aggression intensity, feeding proximity, directional inconsistency index for aggression and grooming)	Call rate Dominance vocal repertoire size	Bayesian Markov chain Monte Carlo generalized linear mixed models		Group size	More tolerant individuals vocalize more frequently More tolerant species have fewer appeasement/dominance vocalizations in their repertoires	(Kavanagh et al. 2019)
		Primates, Strepsirrhines	11	Foraging group size	60 dB high-frequency limits Mean auditory brainstem response threshold	Least-squares regression analysis	Independent contrasts	None	Increased social complexity explained a significant proportion of the variance associated with increased overall auditory sensitivity	(Ramsier et al. 2012)

<u>**Auditory**</u>	**Mammals**	*Fukomys micklemi*	NA	Social system	Vocal repertoire	Descriptive	Closely related species	None	The vocal repertoire of social species is more extensive and diverse than the one of solitary species	(Vanden Hole et al. 2014)
		Subterranean rodents	12	Social vs. solitary	Vocal repertoire	Regression	Phylogenetic independent contrasts	None	The vocal repertoire of social species is larger than the one of solitary species	(Francescoli and Schleich 2019)
		Sciurid rodents	22	Diversity/variability of demographic (age-sex) roles	Alarm call repertoire size	Regression	Independent contrasts, phylogenetic autocorrelation	None	Diversity/flexibility in demographic roles is positively correlated with the alarm call repertoire size	(Blumstein and Armitage 1997)
		Sciurid rodents	8	Social group size	Amount of individuality in alarm calls	Regression	Independent contrasts	None	Contrasts of social group size were significantly correlated with contrasts of individuality in social alarm calls	(Pollard and Blumstein 2011)
		Caviomorph rodent species	7	Group size	Adult vocal repertoire	Linear regression	Independent contrast analysis	None	Positive correlation between group size and adult vocal repertoire size	(Lima et al. 2018)
		Bats	24	Social group size	Individuality in pup isolation calls, adult contact calls and male-specific vocalizations	Regression	SLOUCH	None	Positive relationship between the information content of vocalizations and social group size	(Knörnschild et al. 2020)
<u>**Olfactory**</u>	**Insects**	Hymenoptera, halictid species	36	Ancestral solitary, eusocial, secondarily solitary	Density of sensilla	Phylogenetic generalized least squares analysis	Generalized least square	Host specialization; body size	Significantly higher densities of hair-like sensilla in social species compared with secondarily solitary species	(Wittwer et al. 2017)
		Hymenoptera, *Lasioglossum albipes*	1 (2 behavioral morphs)	Social and solitary behavioral morphs		Comparison of mean	/	Body size	Significantly greater density of sensilla in females from social populations	

Olfactory	**Mammals**	Primates, true lemurs	8	Mating system (pair-bonded, multi-males-multi-females)	Number of chemical compounds in the perianal and genital secretions	Independent t-tests	Closely related species	None	Chemical richness of female perianal secretions was higher in species with MM–MF social systems than in pair-bonded social systems	(delBarco-Trillo et al. 2012)
				Dominance system (co-dominant, female dominance)					Male chemical richness was greater in codominant species than in female-dominant species, both for genital and perianal secretions	
Visual	**Insects**	Wasps *Polistes fuscatus*	25	Nesting strategies flexibility (absence/presence)	Inter-individual variability in facial and abdominal markings	χ2 analysis	Maddison's concentrated changes test	None	Flexibly nesting species are significantly more likely to have variable markings	(Tibbetts 2004)
	Mammals	Primates, Catarhines	139	Group size	Facial color pattern complexity	Multiple regression analysis	Phylogenetic least-squares regression analysis	Number of sympatric species, geographical distribution, ecology	Species living in larger groups have faces with more complex color patterns than species living in smaller groups	(Santana et al. 2013)
		Primates, Catarrhines	12	Social group size	Number of visually distinct facial movements	Multiple regression analysis	Generalized least square	Body-mass, arboreality (generalized least square)	Species living in larger groups tend to produce a greater variety of facial movements	(Dobson 2009)
		Primates, Platyrrhines	199	Group size	Color pattern complexity = total number of uniquely different color areas on the face	Multiple regression analysis	Phylogenetic least-squares regression analysis	Number of sympatric species, geographical distribution, ecology	Species living in smaller groups tended to have faces with more complex patterns than species living in large groups	(Santana et al. 2012)
	Reptiles	Lizards	55	Sexual size dimorphism (SSD), proxy for the intensity of male-male competition	Number of ornaments	Model fitting	Model fitting	Body size, macrohabitat, range (model fitting)	SSD was positively correlated with the number of ornaments	(Ord and Garcia-Porta 2012)

Table I.S2 Summary of studies reporting absence of links between social complexity and communicative complexity. Blue lines were added in this version compared to the published one.

		Taxa (order, genre, species)	Number of species included	Proxy for social complexity	Proxy for communicative complexity	Statistical method	Method for control of phylogeny	Other controlled parameters	Details	Reference
Auditory	**Anurans**	Frogs	32	SSD	Call amplitude modulation Call duration	Model fitting	Model fitting	Sympatry, macrohabitat, microhabitat, noise, body size (model fitting)	There was little support for the role of SSD in the evolution of call amplitude modulation and call duration	(Ord and Garcia-Porta 2012)
	Birds	Birds	23	Extra pair paternity Mating system (monogamy, irregular polygyny, regular polygyny)	Syllable repertoire size Song repertoire size	Model fitting	Model fitting	Macrohabitat, body size, breeding range (model fitting)	There was little support for the role of extra-pair paternity in increasing syllable and song repertoire sizes There was little support for the role of the mating system in increasing syllable and song repertoire sizes	(Ord and Garcia-Porta 2012)
		Birds	253 (59 families)	Group size Cohesiveness of social bonds	Vocal repertoire size	Phylogenetic generalized least squares analysis	Generalized least square	Habitat (generalized least-squares)	Neither group size nor cohesiveness of social bonds significantly influenced repertoire size	(Leighton 2017)

Auditory	**Mammals**	Basal primates (Strepsirrhines & Tarsiers)	22	Social system (solitary, pair, group) Foraging group size	Vocal repertoire size	Kruskal-Wallis ANOVA Multiple regression analysis	None	None	Social system does not significantly impacts affect vocal repertoire size Foraging unit size is not correlated to vocal repertoire size	(Zimmermann 2017)
		Primates	25	Dominance style (counter aggression, aggression intensity, feeding proximity, directional inconsistency index for aggression and grooming)	Vocal repertoire size Social vocal repertoire size	Bayesian Markov chain Monte Carlo generalized linear mixed models		Group size	More tolerant species do not have larger vocal repertoires More tolerant species do not have more social vocalizations in their repertoires	(Kavanagh et al. 2019)
		Baboons genus *Papio*	3	Social system	Repertoire composition	Descriptive	Closely related species	None	Species do not differ in vocal diversity	(Hammerschmidt and Fischer 2019)
		Sciurid rodents	8	Armitage's sociality index Michener's social grade Blumstein and Armitage's social complexity index	Amount of individuality in alarm calls	Regression	Independent contrasts	None	Contrasts of social index were not correlated with contrasts of individuality in social alarm calls Contrasts of social grade were not correlated with contrasts of individuality in social alarm calls Contrasts of social complexity index were not correlated with contrasts of individuality in social alarm calls	(Pollard and Blumstein 2011)

Olfactory	**Insects**	Ants	40	Colony size Mating system (absence/presence of polygyny or polyandry)	Number of different cuticular hydrocarbons (CHC)	Model fitting	Model fitting	Rainfall, temperature (model fitting)	There was little support for the role of colony size and mating system in increasing the number of CHC	(Ord and Garcia-Porta 2012)
		Hymenoptera	133	Social/Solitary	Number of chemical classes Number of CHC isomers	Generalized linear models	None	None	Sociality had no effect on the number of chemical classes nor the number of CHC isomers	(Kather and Martin 2015)
		Hymenoptera	13	Eusocial/Solitary	Chemoreceptor repertoire	Descriptive	Phylogenetic reconstruction	None	The evolution of sociality is not necessarily associated with an increase in the number of odorant receptors	(Zhou et al. 2015)
Visual	**Mammals**	Bats	139	Roosting colony size	Pelage markings	Regression analysis	Phylogenetic logistic regressions	Ecology	Presence of markings was not significantly related to colony size	(Santana et al. 2013)
		Primates, Strepsirrhines	65	Group size	Facial color pattern complexity	Model fitting	Phylogenetic generalized least square regressions	Number of sympatric species, climate	Facial color complexity was independent of group size	(Rakotonirina et al. 2017)
		Hylobatids (*H. moloch, H.pileatus, H.leuconedys*)	4 (10 pairs)	Pair bond strength	Size of facial expression repertoire Facial expression synchrony score	Pearson correlations with Bonferroni correction	None	None	The size of the facial expression repertoire is not significantly correlated with pair-bond strength The facial expression synchrony score is not significantly correlated with pair-bond strength after correction	(Florkiewicz et al. 2018)
	Reptiles	Lizards	22	SSD	Number of head bobbing Duration of display	Model fitting	Model fitting	Body size, microhabitat, macrohabitat, sympatry (model fitting)	There was little support for the role of SSD in increasing display duration and head-bobbing rate	(Ord and Garcia-Porta 2012)

Chapter II: A multimodal approach to communicative complexity in two lemur species having different social systems

Contributions (following CRediT taxonomy): Conceptualization, L.R.P., C.F, and P.M.K.; Methodology, L.R.P.; Formal analysis, L.R.P.; Investigation, L.R.P., B.A., L.A., J.P., P.S, M.R. and C.D.; Resources, L.R.P., C.F and P.M.K.; Writing – original draft preparation, L.R.P.; Writing – review and editing, L.R.P, L.S.M.; Visualization, L.R.P.; Supervision, C.F., and P.M.K.; Funding acquisition, L.R.P., C.F, and P.M.K.

I. Introduction

The “social complexity hypothesis for communicative complexity” (abbreviated SCHCC later in the text) predicts that greater social complexity selects for greater communicative complexity, in both a proximate and ultimate sense (Freeberg et al. 2012a). The rationale behind this hypothesis is that in relatively complex groups, the higher number and diversity of individuals, and the increased number of differentiated relationships among individuals will result in greater uncertainty (Freeberg et al. 2012a; Gero et al. 2016). To navigate this uncertainty, greater communicative complexity will be required to transfer a broader diversity of messages and monitor and manage the behavior of others (Freeberg et al. 2012a; Sewall 2015; Peckre et al. 2019). The social systems usually considered more complex are those having a larger unit size, a greater unit density, and more tolerant individuals (Freeberg et al. 2012a). The SCHCC has been tested in several taxa and garnered a great deal of support (e.g., Blumstein and Armitage 1997; McComb and Semple 2005; May-Collado et al. 2007; Dobson 2009; Leighton 2017; Kavanagh et al. 2019). However, most of these studies provide correlational results revealing a significant relationship between two variables, one single proxy of social complexity and one single proxy for communicative complexity. If these tests have been fruitful, as there is no consensus on what social and communicative complexity are, there is a danger to overlook essential aspects of both social and communicative complexity and to draw false conclusions at the system level (Peckre et al. 2019; Hobson et al. 2019). Indeed, the relationship between social and communicative complexity may occur at different scales. An increase in complexity at the species level may also arise without an increase at the individual level (Aureli and Schino 2019; Hobson et al. 2019). For example, in a society with diverse social roles, individuals may be highly specialized for some specific interactions with a somewhat limited need for signal diversification (Leonhardt et al. 2016). However, at the species level, the multiplication of these social roles may also translate into an increased diversity of signals in the species communicative repertoire. Hence, I argue that a better appreciation of the link between social and communicative complexity may instead be provided by a set of operational measures applicable across taxa (Peckre et al. 2019; Hobson et al. 2019). Conceptualizing communicative complexity along multiple axes and scales may help to generate more accurate predictions about which specific social parameters may be responsible for the selection of new or more complex signals.

According to the most common definitions, communicative complexity can be quantified via two main approaches: the number of distinct signals or signaling units and the number of bits of information included in signals (Griebel and Oller 2008; Pollard and Blumstein 2011; Freeberg et al. 2012a). I argue for the interest of developing and using measures that may be used across taxa based on these two approaches (Peckre et al. 2019). Regarding the first approach, the number of signaling units, the most commonly used measure in the context of the SCHCC is the size of the vocal repertoire (Blumstein and Armitage 1997; McComb and Semple 2005; Gustison et al. 2012; Leighton 2017; Kavanagh et al. 2019). The vocal repertoire size is defined as the number of discrete calls that the animals of one population or species produce. Another standard measure related to this first approach is the call rate. The second approach to communicative complexity is based on the number of bits of information included in signals. This approach, based on information theory, represents a measure of the entropy of a system, which is an estimate of the amount of uncertainty (Cuthill et al. 2017; Fischer et al. 2017b). From a fixed set of signals, more information may first emerge by combinations, either through assemblage (simultaneous expression of different signals) or sequence (succession of different signals) (Bouchet et al. 2013; Manser et al. 2014; Kershenbaum et al. 2016). Vocal sequences have been an intense area of research in studies of birdsong (Kroodsma 2004; Catchpole and Slater 2008), cetaceans (Riesch et al. 2008; Shapiro et al. 2011; Cholewiak et al. 2013; Zwamborn and Whitehead 2017), primates (Clarke et al. 2006; Arnold and Zuberbühler 2008; Zuberbühler and Lemasson 2014; Kershenbaum et al. 2016; Gustison et al. 2016) but also in other mammals such as bats (Kanwal et al. 1994; Bohn et al. 2009) and hyraxes (Kershenbaum et al. 2012).

Group size has been hypothesized to account for the level of complexity of the signaling repertoire, in terms of both size (Blumstein and Armitage 1997; McComb and Semple 2005; Torres Barbosa 2008; Bouchet et al. 2013; Manser et al. 2014) and diversity (Freeberg 2006; Gustison et al. 2019). Particularly, McComb and Semple (2005) found a strong positive correlation between repertoire size and group size ($r=0.58$, $t = 4.52$, $df = 40$, $p<0.001$) across 45 primate species with average group size ranging from 1.5 to 125. Variation in group size for relatively small group sizes, although not considerable, is already likely responsible for essential changes in the nature of the associated relationships. When running the same analysis as McComb and Semple (2005) taking into account only the 18 species with mean group size inferior to ten individuals, the high positive correlation between vocal repertoire size and group size persisted with even a greater coefficient of correlation ($r=0.62$, $t = 3.17$, $df = 16$, $p<0.01$). Besides, it has been suggested that group size may also influence vocal activity (i.e., calling rates; “vocal grooming” hypothesis; Dunbar 1998, 2003; Griebel and Oller 2008; Kulahci et al. 2015). When group size increases, the difficulty of performing “bodily grooming” increases as this behavior can only engage one partner at the time and cannot be combined with other activities such as traveling or foraging. This difficulty is then expected to be compensated by “vocal grooming”.

Species in which social interactions take fairly more predictable forms, through dominance patterns or stable mating associations, were also predicted to have less need for communicative complexity in terms of both signal diversity (Maestripieri 1999) and flexibility (Preuschoft and van Hooff 1995). Indeed, while tolerance is suggested to involve more reversals of interactions and uncertainty regarding the outcomes of social interactions, despotism is suggested to severely limit the extent of possible relationships within a group (Dobson 2009; Kavanagh et al. 2019). Hence, species comprising more tolerant relationships should have more complex communication systems than those involving more despotic relationships.

If most of the tests of the SCHCC considered the acoustic modality, some studies also focused on other modalities, as the visual (Maestripieri 1999, 2005; Dobson 2009; Ord and Garcia-Porta 2012; Molesti et al. 2019) or olfactory ones (Kather and Martin 2015). Indeed, the historical roots of the SCHCC initially predict that the size of the signaling repertoire as a whole should increase with the size of the social group (Lamarck 1873; Marler 1977b). Partan and Marler (2005) mentioned that "Animals communicate with their entire bodies and perceive signals with all available faculties (vision, audition, chemoreception, etc.). To best understand communication, therefore, I must consider the whole animal and all of its sensory emissions and percepts". Yet, in the context of the SCHCC, I am not aware of any study considering signaling repertoires across modalities. Nonetheless, several good reasons exist for acknowledging the multimodal nature of both signals and communicative systems in this framework (Peckre et al. 2019). First, across species, similar social pressures may have led to the evolution of signals of comparable complexity but in different modalities. Second, multimodal signals are, by essence, complex because they involve more than one signaling and perceptive system (Hebets and Papaj 2005). Finally, the flexible use of different modalities permits another level of complexity embedded in multimodal signaling, the many possible combinations of modalities providing a major source of diversity in animal communication systems (Bradbury and Vehrencamp 2011; Waller et al. 2013). Hence, focusing on one modality may lead to over- or underestimation of the relationship between social and communicative complexity at the system level.

In light of the limitations of considering only specific modalities, a holistic approach (i.e., a set of operational measures) and the inclusion of the multimodal aspect of communication are both essential; because similar evolutionary pressures may lead to the evolution of different but equally complex "solutions" (McGhee 2011). For a given set of species, not all aspects of communicative complexity may correspond to the predictions, but possible compensation strategies between different aspects of communicative complexity may occur. Depending on the other selective pressures at play (e.g., ecological), some species may indeed complexify one aspect of their communicative system rather than another (e.g., new signaling units or combinations of these units, signals in one modality or another).

If the measures described so far (i.e., size of the signaling repertoire, rate of expression, number of signal combinations) were all measures already used in the context of the SCHCC, at least in a unimodal context, I propose to prolong this framework offering additional measures at the system level. I specifically argue for the interest of using a cross-modal network approach to signaling systems. This approach is based on the field of phenotypic integration, which aims at understanding the significance of the interrelationships and covariances between trait components (Reichert and Höbel 2018). Within this approach, the response to selection on one characteristic of a given set of correlated characteristics is interpreted as depending on the strength and direction of selection acting on the other characteristics of this same set (Reichert and Höbel 2018). To some extent, signals within a repertoire may also be expected to covary positively or to be subject to conflicting selection pressures to optimize signaling in different contexts (Reichert and Höbel 2018). First, increasing the rate of a signal often entails increasing energetic expenditure leading to a trade-off in the expression of other signals. Second, evolution may select for increased use of multi-component signals, the different components being at least partially under similar selective pressures; this will lead to increased correlations (Reichert and Höbel 2018). Hence, phenotypic integration techniques may help to improve the understanding of the causes and consequences of the evolution of multiple signals within a species repertoire (Reichert and Höbel 2018).

In this framework, I first propose to characterize the level of degeneracy of the system which represents a quantitative measure of how much the signaling behavior of an individual is predictable from only partial information on its signal usage (Wilkins et al. 2015; Hebets et al. 2016; Peckre et al. 2019). The existence of social roles should create consistencies in the behavior of individuals across signals reducing the level of uncertainty faced by an individual (Bergmüller and Taborsky 2010). Second, I propose to characterize the modularity of the system, which informs us about whether this level of uncertainty is more pronounced within or between signaling modalities (Wilkins et al. 2015; Hebets et al. 2016; Peckre et al. 2019). This measure should reveal if the selective pressures at play in shaping the communicative system of the species act predominantly across or within modalities.

We believe that using a cross-modal network approach to signaling systems would offer not only instructive visual representations of multimodal communicative systems but also an opportunity to extract new quantitative and broadly applicable measures that could be interpreted in terms of communicative complexity within and across species. Concretely, applying a cross-modal network approach to animal communication should permit 1) to assess the uncertainty associated with signaling behaviors at the system level (Wilkins et al. 2015; Hebets et al. 2016; Peckre et al. 2019) and 2) allow comparisons at the inter-taxonomic level.

When comparing the size of the signaling repertoires between species, it is of particular interest to study those signals that are structurally unique to a species (hereafter non-homologous signals; equivalent to derived signals in other studies as Gustison et al. 2012; Peckre et al. 2019; Blue 2020). Indeed, these signals that are not shared in the repertoires to compare are the ones that may have been the results of different evolutionary pressures. These signals may be newly derived signals or be more ancestral but conserved in one species and not the other. Identifying the context of emission of these non-homologous signals is therefore of great interest to uncover the selective pressures that originated these divergences (Gustison et al. 2012; Wadewitz et al. 2015; Fischer et al. 2017b). Indeed, rather than an overall increase in repertoire size when comparing species, the increased number of different calls is usually observed in some specific categories (e.g., allospecific and contact calls in meerkats (*Suricata suricatta*; Manser et al. 2014) or affiliative calls in geladas (*Theropethicus gelada*; Gustison et al. 2012). Hence, species having increased group sizes are expected to have a specific increase in affiliative calls, while species with stricter dominance hierarchies are expected to have a specific increase in calls associated with agonistic or submissive calls. Interestingly, looking at two closely related species, chacma baboons (*Papio ursinus*) and geladas (*Theropethicus gelada*), Gustison and colleagues (2012) could show that the non-homologous (derived) call type in geladas functioned in cross-sex bonding and were produced primarily by males. Compellingly, one important difference in the social systems of these two species is that in geladas, males maintain long-term social bonds with females, while in chacma baboons, they only form temporary consortships (Gustison et al. 2012). Hence, looking at specific differences in the communicative system of closely related species having different social systems may help to understand the evolution of communicative complexity and tease apart which are the specific factors driving the emergence or disappearance of specific signals (Gustison et al. 2012, 2019; Bouchet et al. 2013; Molesti et al. 2019; Blue 2020).

Lemurs are interesting because they have retained ancestral characteristics from the earliest primates (Yoder 2007). For instance, they have, as most non-primate mammals, long muzzles, wet noses, and a functional vomeronasal organ and rely heavily on olfactory communication. Most lemurs are also conspicuously vocal and have a well-developed visual sense. Nonetheless, their communication remains poorly studied, especially with a multimodal approach (Slocombe et al. 2011; Norscia and Palagi 2016b). Despite their primitive physical characteristics and relatively small brains, they also have complex and diverse social systems (Oda 2008; Fichtel and Kappeler 2010). Lemurs from Madagascar (Lemuriforms) are the only strepsirrhines having evolved multi-male multi-female groups like those characteristics of most haplorrhines (Fichtel and Kappeler 2010). Among lemurs, the true lemur genus (*Eulemur*) contains twelve different species all endemic to Madagascar, some being group-living, and other pair-living (Markolf and Kappeler 2013; Kappeler and Fichtel 2015) providing excellent models to test the SCHCC.

In this study, I proposed to characterize and compare the complexity of the communicative systems of two true lemur species having different social systems using the framework introduced earlier. I specifically compare the communicative system of the red-fronted lemurs (*Eulemur rufifrons*) with the one of mongoose lemurs (*Eulemur mongoz)*. Red-fronted lemurs live in multimale-multifemale groups of on average 5.4 ± 2.3 individuals while mongoose lemurs live in pairs with their offspring with an average group size of 2.8 ± 0.8 individuals (Kappeler and Fichtel 2015). While *E. mongoz* exhibits female dominance (Curtis and Zaramody 1999), *E. rufifrons* are considered egalitarian, with none of the sex dominating the other and no linear hierarchy within sexes (Pereira et al. 1990; Ostner and Kappeler 2004; Fichtel et al. 2017). Besides these noticeable differences in social organization, these two species exhibit differences in their social system that I summarized in Supplementary Table II.1. Hence, *E. rufifrons* are considered to have a more complex social system than *E. mongoz,* and several predictions can be drawn toward a more complex communicative system in *E. rufifrons* than in *E. mongoz*. These predictions are detailed in Table II.1. If a proper test of the SCHCC would require a quantitative assessment of the social complexity in the species studied during the period of observation considered (Hammerschmidt and Fischer 2019), I believe that the striking differences between the social systems of the two species studied here are significant enough to draw inferences on the effect of socially-related selective pressures on the divergence between these two communicative systems.

Table II.1: Predictions on the expected differences on the different measures of communicative system complexity of *E. mongoz* and *E. rufifrons*

Communicative Parameter	**Prediction**	**Social parameter**	**Hypothesis**
Signaling repertoire size	*E. rufifrons* > *E. mongoz*	Larger group size in *E. rufifrons*	Larger groups will have a greater number of different possible individual-individual interactions and more information to convey so will need an increased number of signals used in affiliative contexts
		Female dominance in *E. mongoz* vs. relative egalitarian society in *E. rufifrons*	Species with stronger dominance patterns will have a greater proportion of signals used in agonistic and submissive contexts in their signaling repertoires
		Pair-bonding maintenance in *E. mongoz* vs. promiscuous mating in *E. rufifrons*	Long-term bonds require familiarity and a subtle coordination of each other's behavior
		Intergroup encounters are rare, short and aggressive in *E. mongoz* vs. regular, long, passive or aggressive in *E. rufifrons*	Species with stronger territorial patterns will have a greater proportion of signals used in agonistic contexts in their signaling repertoires
Signal rate of expression	*E. rufifrons* > *E. mongoz*	Larger group size in *E. rufifrons*	Larger group size will lead to greater call rates (vocal grooming hypothesis)
		Female dominance in *E. mongoz* vs. relative egalitarian society in *E. rufifrons*	Species with more relax dominance and dominant individuals that are more tolerant will vocalized at higher rates
Number of signal combinations	*E. rufifrons* > *E. mongoz*	Larger group size and tolerance levels in *E. rufifrons*	More differentiated relationships in species with larger groups and more relaxed dominance
Modularity of the signal combinations	*E. rufifrons* < *E. mongoz*	Larger group size and tolerance levels in *E. rufifrons*	More complex social environments may favorize multimodal signals
Degeneracy	*E. rufifrons* > *E. mongoz*	Larger group size and tolerance levels in *E. rufifrons*	More differentiated relationships with more fluid social roles will increase uncertainty (increase degeneracy)
Modularity	*E. rufifrons* < *E. mongoz*	Larger group size and tolerance levels in *E. rufifrons*	More complex social environments may favorize signal flexibility across modalities (decrease modularity)

Acknowledging the importance of taking into account phylogeny, anatomy, and ecology when testing the SCHCC (Freeberg et al. 2012a; Ord and Garcia-Porta 2012; Peckre et al. 2019), I here compare closely related species, having relatively similar morphology (body length for body mass: 40-48cm for 2.2-2.3kg in *E. rufifrons* and 30-35cm for 1.1-1.6kg in *E. mongoz*; Mittermeier et al. 2014), living in similar habitats, Madagascar's dry deciduous forests, having similar predators and both exhibiting a cathemeral activity (Tattersall and Sussman 1975; Kappeler and Erkert 2003). Consequently, I expect any observed differences between the communicative systems of these two species to be mainly explained by evolutionary pressures related to social factors while excluding alternative evolutionary forces.

II. Material and methods

1. Subjects and study areas

We collected data on mongoose lemurs (*E. mongoz*) in Ankatsabe forest, an unprotected western dry deciduous forest block situated in the vicinity of Mariarano village, 50 km northwest of Mahajanga, north-western Madagascar. The area is characterized by a wet season peaking in intensity between December and February (mean rainfall of 370mm/month for an average temperature between 24.0-31.5°C over the 1983-2012 period; Direction Générale de la Météorologie de Madagascar 2014) and a pronounced dry season running between June and September (mean rainfall of 1mm/month for an average temperature between 23.8-32.2°C over the 1983-2012 period; Direction Générale de la Météorologie de Madagascar 2014; Palfrey et al. 2019). *E. mongoz* are described as cathemeral, but with some seasonal patterns, nocturnal activity increasing during the dry season (Curtis and Zaramody 1998, 1999). However, across seasons, their activity peaks between 6-8 am, 5-7 pm, and between 11 pm to 2 am. They were also described as particularly inactive during the period comprised between 12 am and 2 pm (Curtis and Zaramody 1999). Potential predators are the fossa (*Cryptoprocta ferox*), dogs, and raptors (Curtis and Zaramody 1998; Evans et al. 2013). The presence of mongoose lemurs in Ankatsabe forest was reported, but no regular study was carried out to date (Long et al. 2010, 2012). I collected data on nine adult mongoose lemurs (four males and five females; Table II.2) belonging to 3 different groups and a solitary male between May and July 2017. A habituation process was necessary; I followed the recommendations provided by (Williamson and Feistner 2003). For more information on this habituation process, see chapter IV. Behavioral seasonality was not described precisely for this species in this population, but based on the literature, the study period was estimated to correspond to their pre-mating season. Indeed (Curtis and Zaramody 1999) reported births in October-November in Anjamena (ca. 60km South-West of Mariarano) while their gestation length is estimated around four months (Zehr et al. 2014). This was later supported by the fact that I did not observe any mating events during our observation period and more concretely by a report of the presence of few months old young in the same population in January 2018 (Bertrand Andriatsitohaina personal communication).

We collected data on red-fronted lemurs in Kirindy Forest, a dry deciduous forest located ca. 60 km north of Morondava, western Madagascar. This area is characterized by a pronounced seasonality similar to the one described for the Mariarano region with a hot, rainy season peaking in intensity between December and February (mean rainfall of 199mm/month for an average temperature between 19.0-31.8°C over the 1983-2012 period; Direction Générale de la Météorologie de Madagascar, 2014) and a colder dry season especially pronounced between June and September (mean rainfall of 1mm/month for an average temperature between 16.6-29.5°C over the 1983-2012 period; (Sorg and Rohner 1996; Direction Générale de la Météorologie de Madagascar 2014). Since 1993, the German Primate Center (DPZ) runs a field station in this forest managed within a forestry concession operated by the Centre National de Formation, d'Etudes et de Recherche en Environnement et Foresterie (CNFEREF). Since 1996, all members of a local population of red-fronted lemurs (*E. rufifrons*) inhabiting a 70-ha study area within the forest have been regularly captured, marked with individual nylon or radio collar, and subjected to regular censuses and behavioral observations. A similar pattern of cathemerality has been described for *E. rufifrons*, with an increase of nocturnal activity in the dry season, and three peaks of activity between 5-9 am 4-6 pm, and 9 pm to 2 am, and a period of inactivity between 10 am and 1 pm (Donati et al. 1999). The main potential predators are as for *E. mongoz*, the fossa (*Cryptoprocta ferox*), dogs, and raptors (Fichtel and Kappeler 2002). Reproduction of the species is seasonal, with a 4-week mating season in May–June and a birth season in September–October (Ostner and Kappeler 1999; Barthold et al. 2009). In 2016, births were reported in this population on September 17th and October 17th (gestation of 120-128 days; Zehr et al. 2014). To assure the best match between the biological seasons of the observations in both species, I selected observations corresponding to their pre-mating season. I collected data on 13 adult red-fronted lemurs (six males and seven females; Table II.2) belonging to 3 different groups from February to May 2016.

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Table II.2: Group composition of the individuals included in the present dataset

Species	Adult males	Adult females	Juveniles
Mongoose lemurs (*E. mongoz*)	1	1	0
	1	2	(1)
	1	2	(1)
	1	0	0
Red-fronted lemurs (E. rufifrons*)*	2(+2)	3	(1)
	2(+1)	3	(3)
	2	1(+1)	(1)

() refer to individuals present in the group but for which data is not available

2. Data collection

We first conducted daily focal recordings. I used a digital solid-state recorder (Marantz PMD 661, Kanagawa, Japan) and a directional microphone (K6 power module, ME66 super-cardioid recording head covered by an MZW 66-PRO velourised foam windshield, Sennheiser, Germany) with a sampling frequency of 48 kHz and a 16-bit amplitude resolution. Additionally, daily 1h focal behavioral observations were carried out to record the signaling behaviors occurring across other modalities (i.e., visual and olfactory). I also commented orally on the occurrence of these signaling behaviors during the recording sessions. Mongoose lemurs were recorded and observed from 6:30 to 10 am and from 3:30 to 6 pm (civil twilight from 5:40-6 am to 5:50-6 pm). Red-fronted lemurs were recorded and observed from 7:30 to 11 am and from 2 to 5 pm (civil twilight from 5:40-6 am to 6-6:50 pm). For each individual, recording and behavioral observation sessions were balanced across time slots. Behavioral observations and recordings were never simultaneously carried out on the same focal individual.

3. Data analyses

All analyses were performed using R version 3.6.2 (R Core Team 2019).

a. Signaling rates

For each audio file, I annotated each call using Avisoft SASLab Pro software (Pellissier et al. 2018). I identified 2221 calls from the mongoose lemurs and 3772 calls from the red-fronted lemurs. I classified the different call types visually. For each focal recording and each call type, I calculated a rate (number of occurrences per hour). For the behavioral observations, I included 130h of focal observations for *E. mongoz* (from 10 to 20h per individual) and 123h for *E. rufifrons* (from 6 to 19h per individual). For each focal behavioral observation session and each visual and olfactory behavior, I calculated a rate (number of occurrences per hour). I then averaged these rates for each individual across the different focal recordings or observation sessions to obtain individual values for each signaling behavior. Individual signaling rates were later averaged by sex and species and compared using unpaired two-sample Wilcoxon tests.

b. Signaling networks construction

I built signaling networks in which each node represents a different signal. Node shape and color were attributed based on the primary sensory channel involved (dominant modality) corresponding to each signal (Table II.3 & Table II.4). Each edge of the network represents Spearman's ρ correlations between the individual rates of expression of the signals it connects. Correlation magnitude and directions are denoted by the size and the color of the edges. To minimize the interpretation of incidental correlations due to the individuals sampled, I calculated 1000 bootstrapped correlation coefficients and discarded any resultant correlation whose confidence interval overlapped zero (Supplementary Figure II.1 & Supplementary Figure II.2). This method applied by Wilkins and colleagues (2015) allows me to remove non-robust correlation estimates that may be influenced by a single individual. Networks were plotted using the package "qgraph" (version 2.0.1; Epskamp et al. 2012).

c. Measures of signaling network properties

For both species, I assessed the levels of degeneracy (i.e., uncertainty) and modularity of their signaling network, including only all robust edges (non set to 0 after bootstrapping).

To assess degeneracy (Hebets et al. 2016), I used two measures: average correlation strength and network density. The average correlation was calculated as the mean of the absolute values of the correlation matrix (excluding correlations set to 0). Network density was measured by the number of robust edges divided by the total number of possible pairwise correlations. Larger values of average correlation and network density correspond to a lower level of system degeneracy (i.e., less uncertainty). Significance was obtained by calculating where the observed measure value falls relative to the distribution of the measure values obtained with 1000 null models (number of times it was greater or lower divided by the number of null datasets used; Supplementary Figure II.3-Supplementary Figure II.6; Farine 2017). Null models were obtained by applying the bootstrapping procedure described above on datasets, where the values of the signaling rates were randomized. For each signal, random rate values from a uniform distribution ranging between the minimum and maximum values observed in the real dataset were attributed to each individual.

To measure the degree of modularity of the networks, I calculated the weighted assortativity coefficient using the "assortnet" package (Farine 2016). Significance was obtained by calculating where the observed measure value falls relative to the distribution of the levels of assortativity obtained with 1000 null models (Supplementary Figure II.7 & Supplementary Figure II.8). These null models were randomized networks generated by permuting the attributed modality across signals (Wilkins et al. 2015; Farine 2016). If correlations within a modality are stronger than correlations across modalities, then assortativity should be greater than the random expectation. If correlations across modalities are stronger than correlations within a modality, then assortativity should be significantly lower than the random expectation.

d. Comparing signaling network properties between species

Because network measures are sensible to sampling issues (i.e., sampling effort, signal diversity), network properties measures cannot be directly compared. Here I propose to compare the three network properties measures (i.e., average correlation, network density, and assortativity) using two different methods. First, I used a rarefaction analysis to take into account the effect of the different number of nodes (i.e., signals) between the two species (Pellissier et al. 2018). I removed signals randomly from the larger network, the one of *E. rufifrons*, to match the size of the smaller one, the one of *E. mongoz,* and repeated my measurements on this new network. This procedure was repeated 1000 times in order to obtain a statistical distribution of the measures based on these rarefied networks. I then compared for each measure independently, the observed value for the signaling network of *E. mongoz* to the distribution of the measures based on the rarefied *E. rufifrons* signaling networks (Pellissier et al. 2018). Second, I calculated, for each measure independently, pairwise differences between the values obtained from the null models generated by randomizing the signaling rates in both species (see section c. above). I then compared the observed difference (value for *E. mongoz* minus value for *E. rufifrons*) to the distribution of the differences obtained with the null models (Farine 2017).

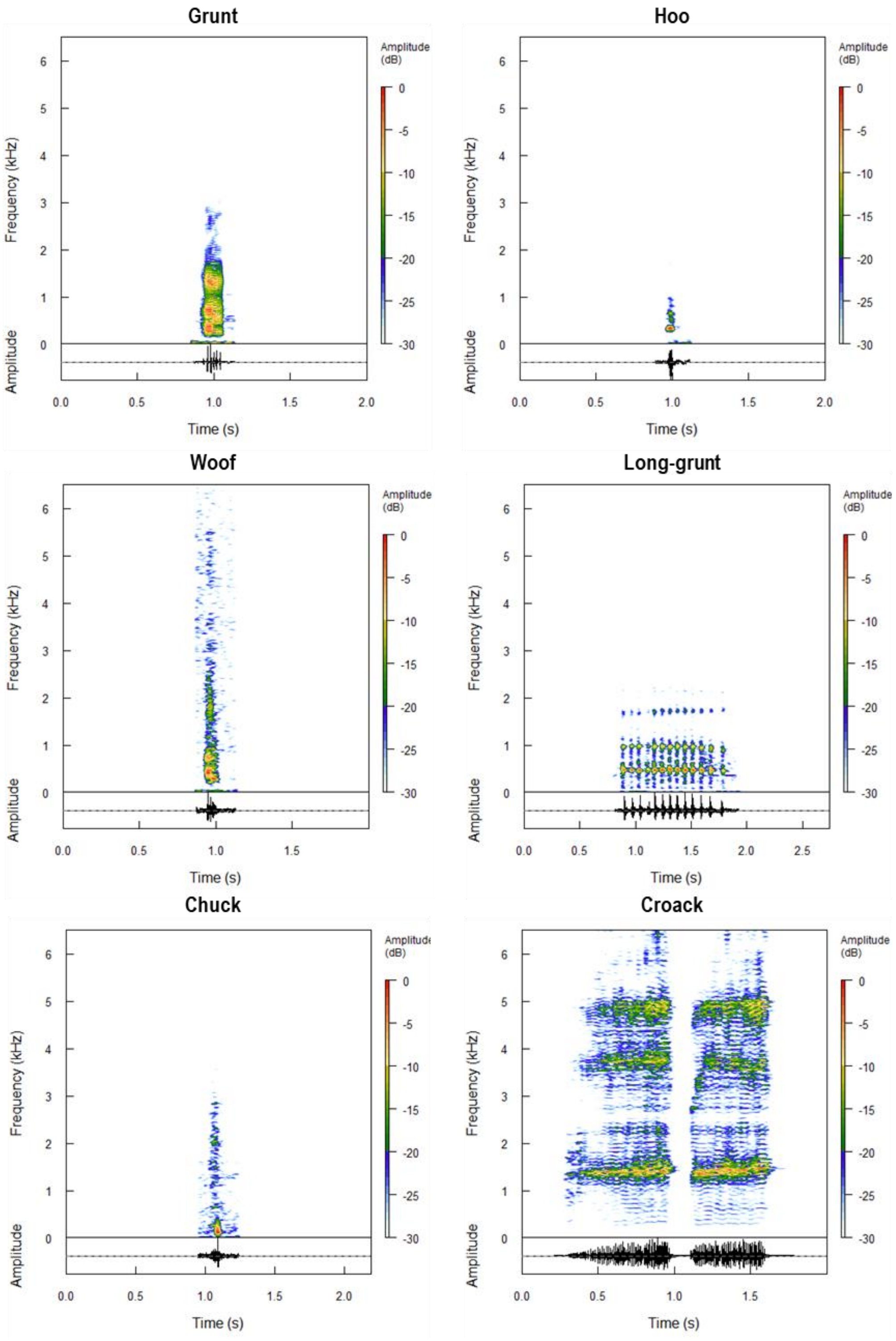
e. *Assessing the number of signal combinations (assemblages and sequences)*

Additionally, I look at the temporal associations between the different signals. I created signal combinations probability matrices for two timeframes, 0 to 1 s and 1 to 60 s. These probability matrices are based on the probability for each signal to be associated with each other signal from the species repertoire. The sum of the probabilities for each row represents the probability for this signal to be associated with another one in the given timeframe. Signals associated in the 0 to 1 s time window were considered signal assemblages while signals associated in the 1 to 60 s time window were considered signal sequences; both are here considered as signal combinations. I first report the number of non-null probabilities for each matrix, these numbers corresponding to the number of different assemblage and sequence types for each species. I then built directed weighted networks in which each node is a signal, and each edge is the probability of combination. For each of these networks, I reported the observed average probability, density, and assortativity measures (calculated as described in section c).

III. Results

1. Size of the signaling repertoires

I identified six acoustic, three olfactory, and four visual signals in *E. mongoz* (Figure II.1 & Table II.3) while I observed 12 acoustic, seven olfactory, and five visual signals in *E. rufifrons* (Figure II.2 & Table II.4). All signals observed in *E. mongoz* were also observed in *E. rufifrons*. One call type, the croack, was never produced by the focal individual during the focal recording sessions of *E. rufifrons* but was recorded from non-focal individuals. Similarly, two olfactory behaviors, the anogenital scent-marking of a partner and palmar rubbing, were also observed and reported during the recording sessions but never during the behavioral observations. These three signals were then included in the signaling repertoire of the species but did not appear in subsequent analyses.


Grunt

Hoo

Woof

Long-grunt

Chuck

Croack

Figure II.1: Sound spectrograms representation illustrating the 6 call types identified visually in the *E. mongoz* recordings. These spectrograms were generated in R using the "seewave" package (Sueur et al. 2008) using the following parameters: window length: 1024; sampling frequency: 16kHz; Fourier transform window: "hanning"; overlap between the successive windows: 87.5%

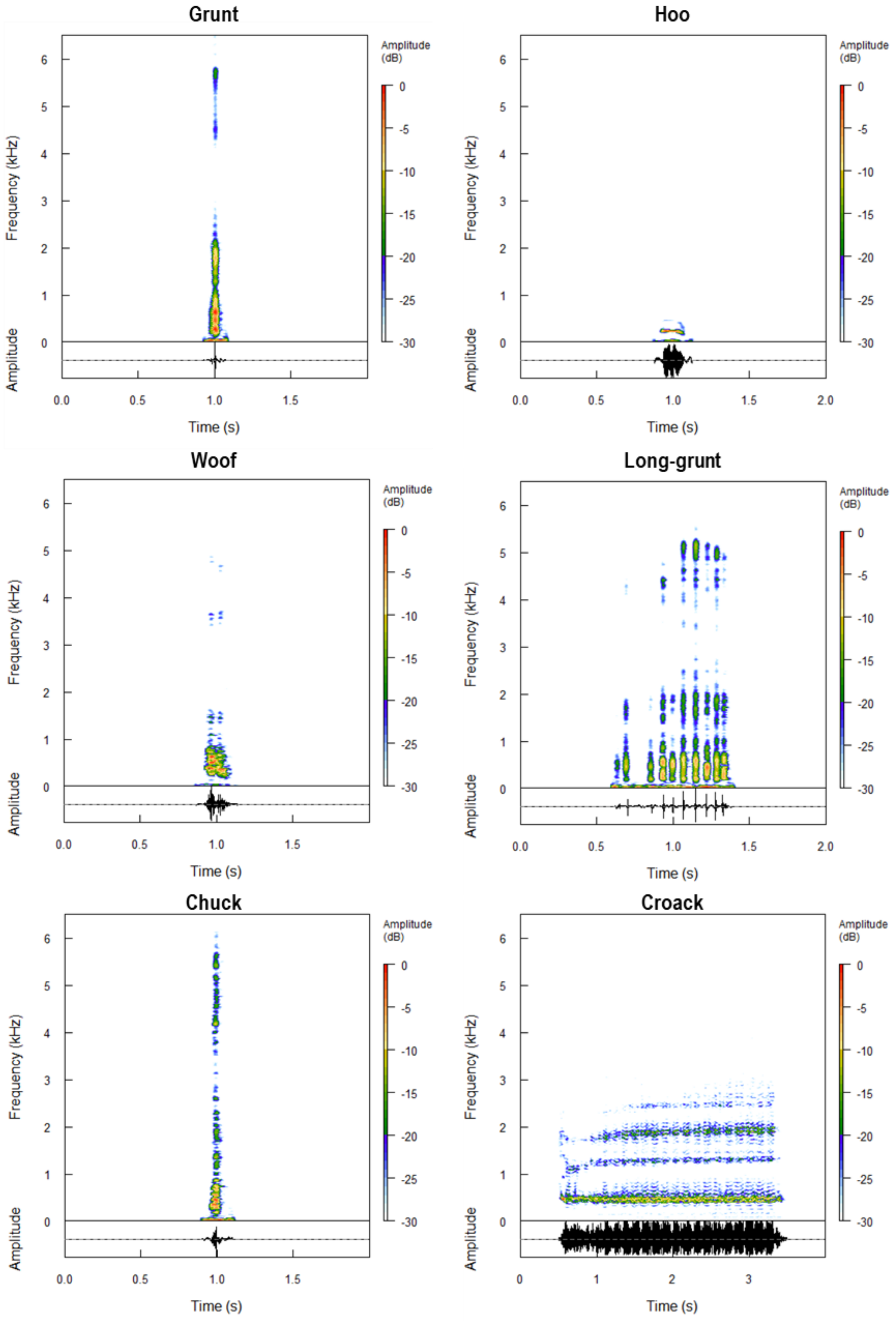


Figure II.2: Sound spectrograms representations illustrating the 12 call types identified visually in the *E. rufifrons* recordings. These spectrograms were generated in R using the "seewave" package (Sueur et al. 2008) using the following parameters: window length: 1024; sampling frequency: 16kHz; Fourier transform window: "hanning"; overlap between the successive windows: 87.5%

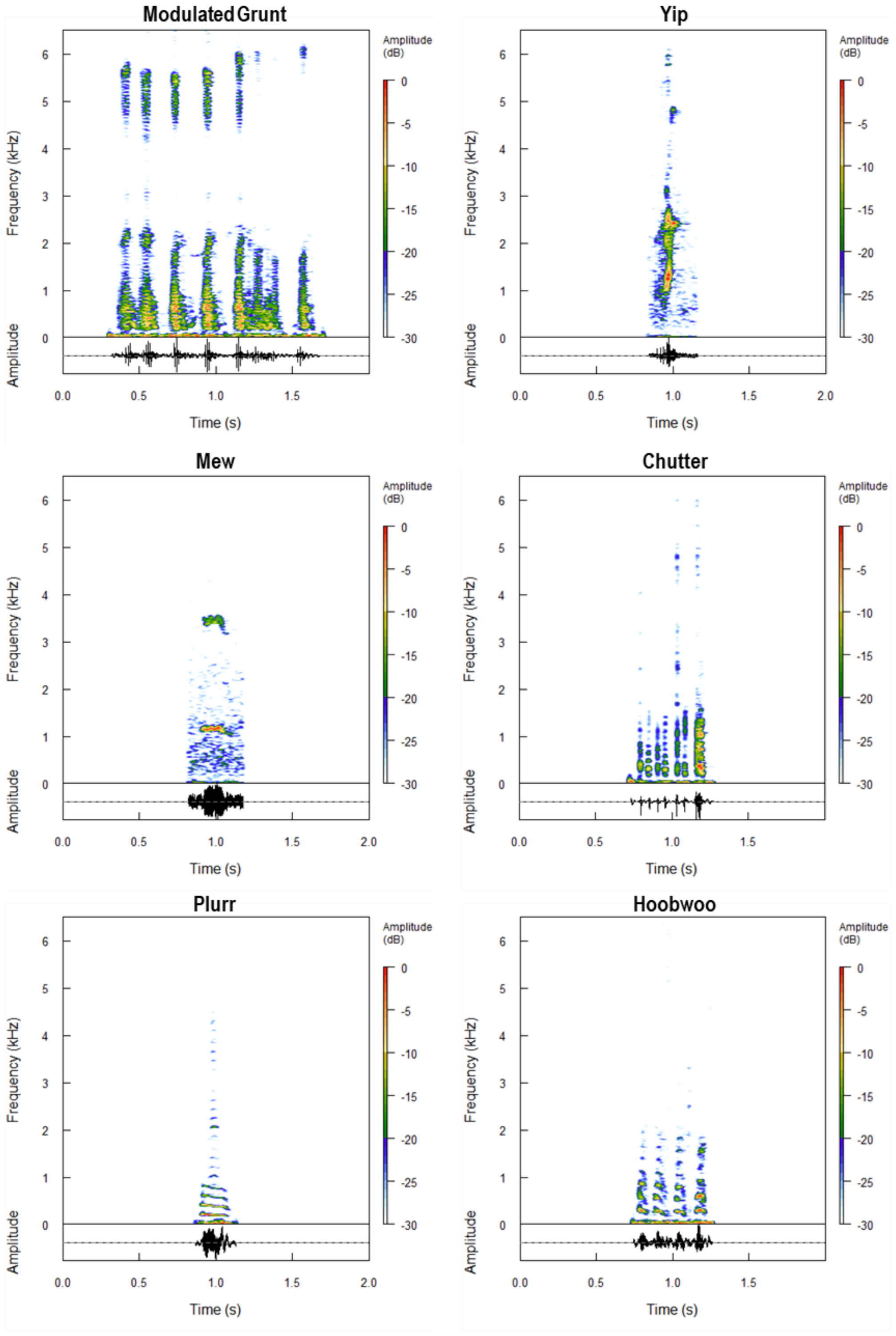


Figure II.2: (continued) Sound spectrograms representations illustrating the 12 call types identified visually in the *E. rufifrons* recordings. These spectrograms were generated in R using the "seewave" package (Sueur et al. 2008) using the following parameters: window length: 1024; sampling frequency: 16kHz; Fourier transform window: "hanning"; overlap between the successive windows: 87.5%

Table II.3: Description of the 13 signals identified in *E. mongoz*.

	Name (abr.)	Homologous signal (Y/N)	Description	Context	Context type	Rate (#/hour)	References
Acoustic	**Chuck (Chu)**	Yes	Very short, plosive harmonic call	Aerial alarm call	Allospecific	0.24±0.24 (♀ 0.44±0.44; ♂ 0±0)	"Aerial alarm call" (Nadhurou et al. 2015); "cak" (Curtis and Zaramody 1999)
	Croack (Cro)	Yes	Loud, trilled, noisy calls	Between-group communication, group cohesion when an individual is isolated from its group, in presence of terrestrial predators High levels of arousal	Allospecific or social (long-range), intragroup and intergroup levels	0.3±0.2 (♀ 0.53±0.33; ♂ 0±0)	"Territorial calls" (Nadhurou et al. 2015); "creeee" (Petter and Charles-Dominique 1979); "terrestrial disturbance" (Macedonia and Stanger 1994); "screech" (Curtis and Zaramody 1999); "rasp" (Tattersall and Sussman 1975)
	Grunt (Gru)	Yes	Short, low-pitched, low amplitude, guttural, noisy pulse	Group coordination: group movement, foraging, intergroup encounters Low emotional intensity	Social (close-range), intragroup level	31.75±9.4 (♀ 30.61±10.89; ♂ 33.17±18.2)	"grunt" or "Grunt clear call" or "grunt hoot" (Nadhurou et al. 2015); "medium-intensity alarm calls" (Petter and Charles-Dominique 1979); "grunt" or "explosive grunt" (Tattersall and Sussman 1975); "grunt sneeze" (Curtis and Zaramody 1999)

	Long-grunt (LGru)	Yes	Sequence of low-pitched pulsed units	Group cohesion during traveling, intergroup encounters, sudden disturbance Intermediate level of arousal	Allospecific or social (close-range), intragroup and intergroup levels	3.32±2.7 (♀ 5.56±4.84; ♂ 0.52±0.17)	“Long-grunt” or “open mouth grunt” (Macedonia and Stanger 1994); “Alarm long-grunt” or “Long-grunt” (Nadhurou et al. 2015); “Creeeee” or “greee” (Petter and Charles-Dominique 1979); “creak” or “long creak” (Curtis and Zaramody 1999); “creaking door” (Tattersall and Sussman 1975)
	Hoo (Hoo)	Yes	Brief harmonic emission of low amplitude and scant frequency modulation, Guttural	Exchange between several individuals while resting	Social (close-range), intragroup level	4.35±2.4 (♀ 6.19±4.04; ♂ 2.04±2.04)	Hoot (Macedonia and Stanger 1994; Nadhurou et al. 2015); “sneeze” (Petter and Charles-Dominique 1979; Curtis and Zaramody 1999)
	Woof (Woo)	Yes	Grunt with noisy terminus, resemble human sneeze	Group encounters, terrestrial predators Higher emotional arousal	Allospecific or social (close-range), intergroup level	4.45±2.55 (♀ 6.37±4.42; ♂ 2.04±1.73)	“Snort” (Petter and Charles-Dominique 1979; Curtis and Zaramody 1999; Nadhurou et al. 2015); “explosive grunt” (Tattersall and Sussman 1975)
Olfactory	**Anogenital-mark (Gm)**	Yes	Rubbing anogenital region on a substrate	Intergroup encounter; pair-bonding especially around mating	Social, intragroup and intergroup levels	0.12±0.08 (♀ 0.01±0.01; ♂ 0.26±0.15)	(Tattersall and Sussman 1975; Harrington 1978; Curtis and Zaramody 1999; Colquhoun 2011)
	Head-rub* (Hm)	Yes	Rubbing forehead on a substrate	Intergroup encounter; pair-bonding especially around mating	Social, intragroup and intergroup levels	0.08±0.06 (♀ 0±0; ♂ 0.17±0.14)	(Tattersall and Sussman 1975; Harrington 1978; Curtis and Zaramody 1999; Colquhoun 2011)
	Urinate (Ur)	Yes	Lower hindquarters and deposit dribble of urine on a substrate	Group encounter	?	0.05±0.02 (♀ 0.05±0.03; ♂ 0.05±0.02)	(Colquhoun 2011)

Visual	**Scratching (Sc)**	Yes	Animal scratches itself	-	?	1.83±0.35 (♀ 1.51±0.32; ♂ 2.24±0.68)	-
	Self-grooming (Sg)	Yes	Animal grooms itself	-	?	3.55±0.42 (♀ 3.13±0.43; ♂ 4.08±0.75)	-
	Tail-waving (Tl)	Yes	Swing tail from side-to-side	Human, terrestrial predator (snakes), group encounter, general disturbance	Allospecific or social (close-range), intergroup level	1.2±0.45 (♀ 1.15±0.67; ♂ 1.27±0.66)	(Tattersall and Sussman 1975; Harrington 1978; Curtis and Zaramody 1999)
	Yawn (Ya)	Yes	Stretch mouth wide open without vocalizing	-	?	0.05±0.02 (♀ 0.01±0.01; ♂ 0.09±0.05)	-

*indicate male-specific signals

Table II.4: Description of the 24 signals identified in *E. rufifrons*.

Acoustic	**Chuck (Chu)**	Yes	very short, plosive harmonic call	Aerial predators	Allospecific (close-range)	1.08±0.41 (♀ 1.07±0.52; ♂ 1.09±0.71)	(Pereira and Kappeler 1997)
	Chutter# (Cht)	No	Rapid series of loud, noisy syllables	Aerial predators, aggressive intergroup conflicts	Allospecific or social (long-range), intergroup level	0.76±0.76 (♀ 1.41±1.41; ♂ 0±0)	(Pereira and Kappeler 1997; Fichtel and Kappeler 2002)
	Croack (Cro)	Yes	Loud, trilled, noisy calls Long-range	Between-group communication, group cohesion when an individual is isolated from its group, in presence of terrestrial predators High levels of arousal	Allospecific or social (long-range), intragroup and intergroup levels	/	(Petter and Charles-Dominique 1979; Macedonia and Stanger 1994; Pereira and Kappeler 1997)
	Grunt (Gru)	Yes	Short, low-pitched, low amplitude, guttural, noisy pulse	Group coordination: group movement (recruitment function), foraging, facilitate peaceful social interactions, intergroup encounters Low emotional intensity	Social (close-range), intragroup level	364.31±67.54 (♀ 328.91±65.78; ♂ 405.61±130.49)	(Pereira and Kappeler 1997; Pflüger and Fichtel 2012; Sperber et al. 2017)
	Long-grunt (LGru)	Yes	Sequence of low-pitched pulsed units Short-range	Group cohesion during traveling, intergroup encounters, sudden disturbance Intermediate level of arousal	Allospecific or social (close-range), intragroup level	9.7±6.19 (♀ 6.84±5.29; ♂ 13.04±12.48)	(Pereira and Kappeler 1997; Pflüger and Fichtel 2012)

	Modulated-grunt# (MGr)	No	Long-grunt with rapid amplitude modulation	Greeting behavior	Social (close-range), intragroup level	1.42±0.6 (♀ 1.64±0.84; ♂ 1.17±0.93)	(Pereira and Kappeler 1997)
	Hoo (Hoo)	Yes	Brief harmonic emission of low amplitude and scant frequency modulation, Guttural	Exchange between several individuals while resting	Social (close-range), intragroup level	9.39±6.02 (♀ 3.69±2.2; ♂ 16.04±12.85)	(Pereira and Kappeler 1997; Pflüger and Fichtel 2012)
	Hoob-woo# (Hwo)	No	Rapid series of short, soft, tonal syllables	While rushing toward social partner, grooming	Social (close-range), intragroup level	0.97±0.48 (♀ 0.28±0.28; ♂ 1.79±0.91)	(Pereira and Kappeler 1997)
	Meow# (Mew)	No	Quiet, brief, high-pitched, tonal monosyllable	Group movements	Social (long-range), intragroup level	1.08±0.89 (♀ 1.81±1.65; ♂ 0.23±0.23)	(Pereira and Kappeler 1997; Pflüger and Fichtel 2012)
	Plurr# (Plu)	No	Quiet, breathy monosyllable	During play	Social (close-range), intragroup level	1.84±0.84 (♀ 2.08±1.16; ♂ 1.55±1.31)	(Pereira and Kappeler 1997)
	Woof (Woo)	Yes	Grunt with noisy terminus, resemble human sneeze	Terrestrial predators, intergroup encounters Higher emotional arousal	Allospecific or social (close-range), intergroup level	60.87±38.28 (♀ 91.72±70.73; ♂ 24.89±11.57)	"Woof" or "Huvv" (Pereira and Kappeler 1997; Fichtel and Kappeler 2002; Fichtel and Hammerschmidt 2002)
	Yip# (Yip)	No	Short, piercing, high-pitched call	-	Social (long-range), intragroup level	10.14±5.05 (♀ 5.32±3.18; ♂ 15.76±10.34)	"Yipe" (Pereira and Kappeler 1997)
Olfactory	**Anogenital-mark (Gm)**	Yes	Rubbing anogenital region on a substrate	Intergroup encounters, intragroup communication	Social, intragroup and intergroup levels	0.48±0.1 (♀ 0.5±0.14; ♂ 0.45±0.15)	(Pereira and Kappeler 1997; Gould and Overdorff 2002; Colquhoun 2011; chapter IV)
	Anogenital-mark partner*	No	Rubbing anogenital region on another individual	Intergroup encounters, intragroup communication	Social, intragroup and intergroup levels	/	(Pereira and Kappeler 1997; Gould and Overdorff 2002; Colquhoun 2011)

	Bite marking#* (Chw)	No	Chew branches while salivating	/	?	0.01±0.01 (♀ 0±0; ♂ 0.03±0.03)	(Colquhoun 2011)
	Head-rub* (Hm)	Yes	Rubbing forehead on a substrate	Intergroup encounters, intragroup communication	Social, intragroup and intergroup levels	0.05±0.02 (♀ 0±0; ♂ 0.1±0.04)	(Pereira and Kappeler 1997; Gould and Overdorff 2002; Colquhoun 2011)
	Head-rub partner#* (Hmp)	No	Rubbing forehead on another individual	Intergroup encounters, intragroup communication	Social, intragroup and intergroup levels	0.01±0.01 (♀ 0±0; ♂ 0.02±0.02)	(Pereira and Kappeler 1997; Gould and Overdorff 2002; Colquhoun 2011)
	Palmar rubbing	No	Rub palms repeatedly around stick or branch	Associated with head-rubbing	Social	/	(Gould and Overdorff 2002; Colquhoun 2011)
	Urinate (Ur)	Yes	Lower hindquarters and deposit dribble of urine on a substrate	Group encounters	Social, intergroup level	0.08±0.03 (♀ 0.08±0.04; ♂ 0.08±0.05)	(Pereira and Kappeler 1997; Colquhoun 2011)
Visual	**Flick-tongue#* (Tfl)**	No	Extend tongue from nearly-closed mouth 2-10 times in 3-4 s (Figure II.3)	Greeting behavior	Social (close-range), intragroup level	0.03±0.03 (♀ 0±0; ♂ 0.06±0.06)	(Pereira and Kappeler 1997)
	Scratching (Sc)	Yes	Animal scratches itself	-	?	2.85±0.47 (♀ 2.77±0.24; ♂ 2.94±1.04)	-
	Self-grooming (Sg)	Yes	Animal grooms itself	-	?	4.65±0.71 (♀ 4.48±0.49; ♂ 4.84±1.51)	-
	Tail-waving (Tl)	Yes	Swing tail from side-to-side (Figure II.4)	Terrestrial predators, group encounters	Allospecific or social (close-range), intergroup level	0.05±0.02 (♀ 0.06±0.04; ♂ 0.03±0.02)	(Fichtel and Hammerschmidt 2002) "Tail pendulum" (Pereira and Kappeler 1997)
	Yawn (Ya)	Yes	Stretch mouth wide open without vocalizing		?	0.19±0.07 (♀ 0.16±0.08; ♂ 0.23±0.12)	(Pereira and Kappeler 1997)

indicate non-homologous signals; * indicate male-specific signals

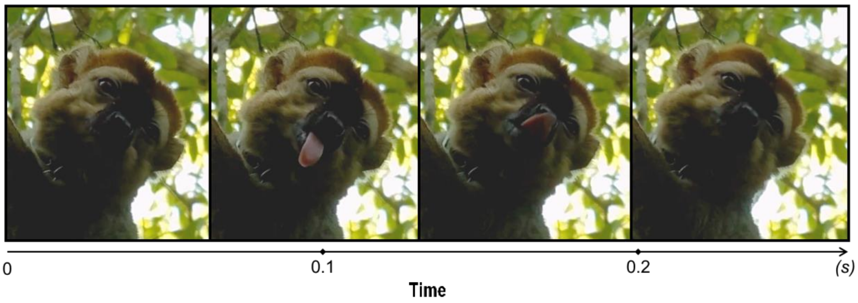


Figure II.3: Illustration of the "flick-tongue" signal observed in males *E. rufifrons*

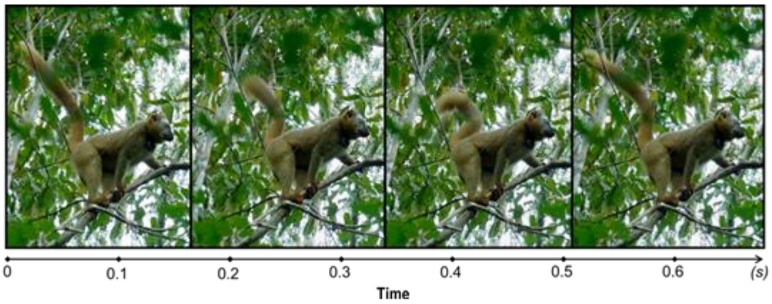


Figure II.4: Illustration of the "tail-waving" signal; case of a female *E. rufifrons*

2. Signaling rates

The average acoustic and olfactory signaling rates were significantly lower in *E. mongoz* than in *E. rufifrons* (E.m: 44.4 ± 4.0 vs. E. r: 461.6 ± 24.6 calls per hour; unpaired two-sample Wilcoxon tests: W=5; <0.001 and E.m: 0.2 ± 0.0 vs. E.r: 0.6 ± 0.0 olfactory signals per hour; unpaired two-sample Wilcoxon tests: W=25.5; p=0.03). The average rate of visual signals was not significantly different between the two species (E.m: 6.6 ± 0.3 vs. E.r: 7.8 ± 0.3 visual signals per hour; unpaired two-sample Wilcoxon tests: W=49; p=0.556). Signaling rates for each signal and each sex are presented in Table II.3 & Table II.4. Among the homologous signals, significant differences in signaling rates were found between the two species for 5 out of the 12 signals compared (Figure II.5). Males and females *E. rufifrons* grunted significantly more often than *E. mongoz* (♀ E.m: 30.61±10.89 vs. ♀ E.r: 328.91±65.78; unpaired two-sample Wilcoxon tests: W=0; p=0.003 and ♂ E.m: 33.17±18.2 vs. ♂ E.r: 405.61±130.49; unpaired two-sample Wilcoxon tests: W=1; p=0.019; Figure II.5). Females red-fronted lemur were also observed to anogenital-mark (♀ E.m: 0.01±0.01 vs. ♀ E.r: 0.5±0.14; unpaired two-sample Wilcoxon tests: W=3; p=0.018), scratch (♀ E.m: 1.51±0.32 vs. ♀ E.r: 2.77±0.24; unpaired two-sample Wilcoxon tests: W=4; p=0.03) and yawn (♀ E.m: 0.01±0.01 vs. ♀ E.r: 0.16±0.08; unpaired two-sample Wilcoxon tests: W=4; p=0.029) significantly more often than females mongoose lemur (Figure II.5). However, tail-waving was significantly more often exhibited by both males and females *E. mongoz* than by *E. rufifrons* (♀ E.m: 1.15±0.67 vs. ♀ E.r: 0.06±0.04; unpaired two-sample Wilcoxon tests: W=33; p=0.012 and ♂ E.m: 1.27±0.66 vs. ♂ E.r: 0.03±0.02; unpaired two-sample Wilcoxon tests: W=23; p=0.021; Figure II.5).

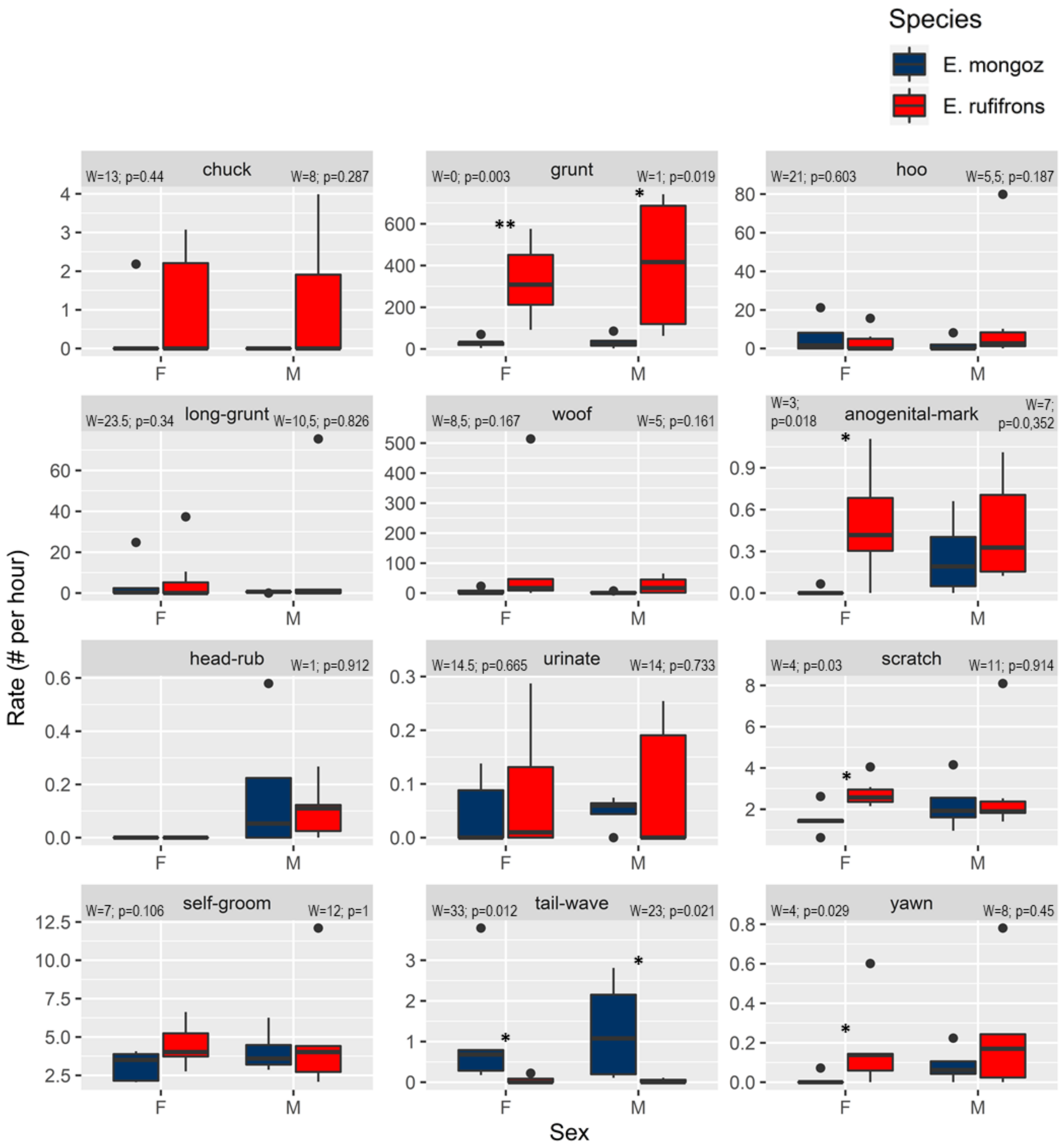


Figure II.5: Rates of expression (occurrence per hour) of each signal present in both *E. mongoz* and *E. rufifrons*. * indicate a significant Wilcoxon test with a p-value<0.05 and ** indicate a significant Wilcoxon test with a p-value <0.01. Sample sizes are of 5 females and 4 males *E. mongoz* and 7 females and 6 males *E. rufifrons*.

3. Measures of signaling network properties: degeneracy and modularity

Degeneracy measures were |avg corr|= 0.54 (p<0.001; Figure II.6 .1; Supplementary Figure II.3) and network density = 0.31 (p<0.001; Figure II.6 .1; Supplementary Figure II.5) for *E. mongoz* and |avg corr| = 0.31 (p<0.001; Figure II.6 .2; Supplementary Figure II.4) and network density = 0.27 (p<0.001; Figure II.6 .2; Supplementary Figure II.6) for *E. rufifrons* (Table II.5). The average correlation measure of the signaling network of *E. mongoz* was significantly greater than the one observed for the signaling network of *E. rufifrons* (p=0.01 with the rarefaction test and p=0.011 with the null-models comparison test; Figure II.7 & Figure II.8; Table II.5). Network density did not significantly differ between the two species (p=0.405 for the rarefaction comparison test, Figure II.7, and p=0.166 for the null-models comparison test, Figure II.8; Table II.5).

Table II.5: Comparison of the signaling networks properties measures of *E. mongoz* and *E. rufifrons*

		Species		**Species comparisons**	
	Measure	***E. mongoz***	***E. rufifrons***	**Rarefaction**	**Null models**
Degeneracy	|avg corr|	0.54 (p<0.001)	0.31 (p<0.001)	p=0.01	p=0.011
	network density	0.31 (p<0.001)	0.27 (p<0.001)	p=0.405	p=0.166
Modularity	Assortativity coefficient (r_d ± jackknife s.e.)	0.15 ± 0.16 (p= 0.036)	0.02 ± 0.08 (p= 0.144)	p=0.097	p=0.14

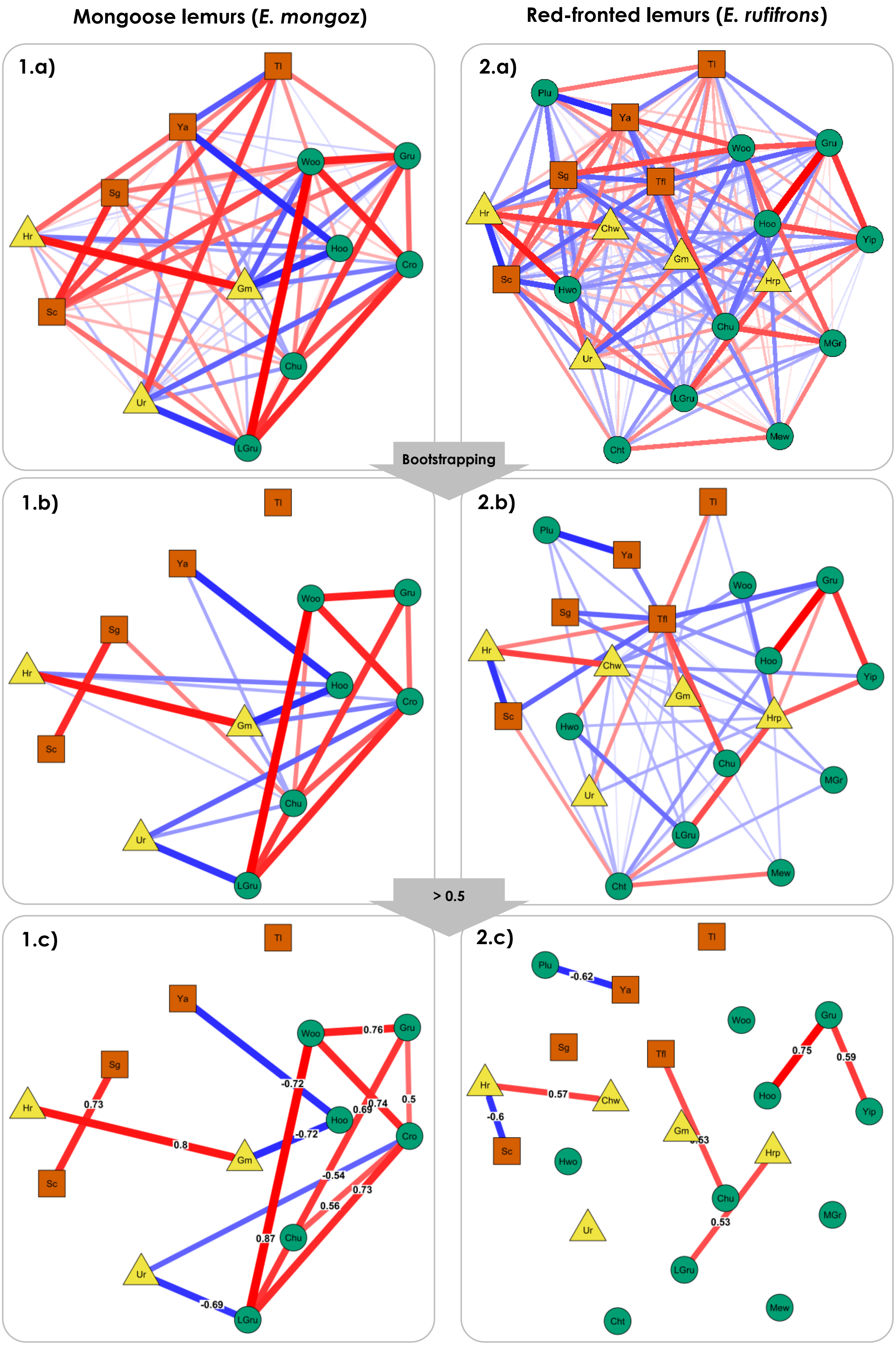

Mongoose lemurs (*E. mongoz*)
Red-fronted lemurs (*E. rufifrons*)
1.a)
2.a)
Bootstrapping
1.b)
2.b)
> 0.5
1.c)
2.c)
Tl
Ya
Sg
Hr
Sc
Gm
Ur
Woo
Gru
Hoo
Cro
Chu
LGru
Plu
Tfl
Chw
Hwo
Yip
Hrp
MGr
Cht
Mew
-0.72
0.76
0.73
0.69
0.74
0.5
0.8
-0.72
-0.54
0.73
0.56
0.87
-0.69
-0.62
0.75
0.59
0.57
-0.6
0.53
0.53

Figure II.6 (precedent page): Signaling networks of **1.** *E. mongoz* and **2.** *E. rufifrons* with **a)** raw data **b)** after bootstrapping procedure on the individuals (n=1000 iterations) and **c)** after the same bootstrapping procedure but restricted to correlations above 0.5. Each node shape and color correspond to a different signaling modality: green circles for vocal signals; yellow triangles for olfactory signals and orange squares for visual signals. Chu=Chuck; Cht=Chutter; Cro=Croack; Gru=Grunt; LGru=Long-grunt; MGr=Modulated-grunt; Hoo=Hoo; Hwo=Hoob-woo; Mew=Mew; Plu=Plurr; Woo=Woof; Yip=Yip; Chw=Chew branch; Gm=Anogenital-mark; Hr=Head-rub; Hrp=Head-rub partner; Ur=Urinate; Tfl=Flick-tongue; Sc=Scratching; Sg=Self-grooming; Tl=Tail-waving; Ya=Yawn. Correlation magnitude and directions are denoted by the size and the color of the lines connecting the different signals: blue lines indicate negative correlations while red lines indicate positive ones

The assortativity coefficient (r_d ± jackknife s.e.) was 0.15 ± 0.16 for *E. mongoz* and 0.02 ± 0.08 for *E. rufifrons* (Figure II.6 ; Table II.5). While for *E. rufifrons*, the assortativity coefficient was not greater or lower than expected under random assortment (p= 0.144; Supplementary Figure II.8), it was significantly greater than expected under random assortment for *E. mongoz* (p= 0.036; Supplementary Figure II.7). However, assortativity did not appear to differ significantly between both species (p=0.097 for the rarefaction comparison test, Figure II.7, and p=0.14 for the null-models comparison test, Figure II.8; Table II.5).

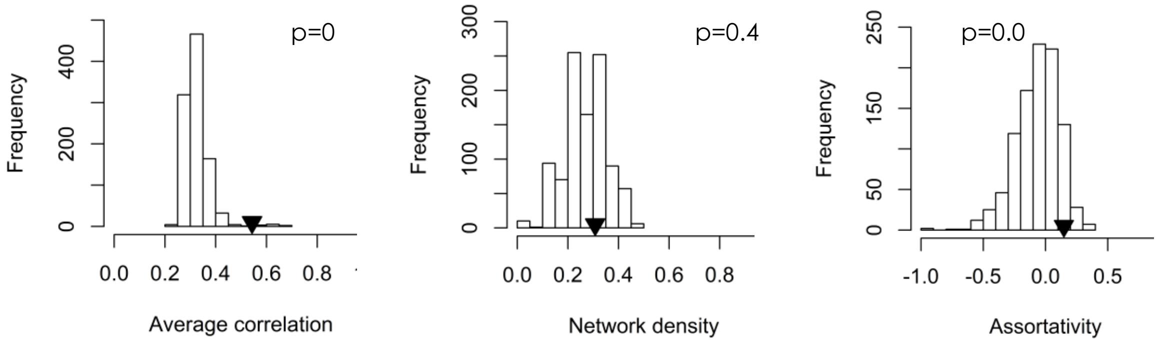


Figure II.7: Network properties measure values of *E. rufifrons* calculated from 1000 null models. The empirical values for *E. mongoz* are shown as black triangles. The measure of average correlation obtained for *E. mongoz* is significantly greater than the ones obtained for *E. rufifrons* (p=0.01) but the values of network density and assortativity of *E. mongoz* are not different from the one observed by rarefaction of the *E. rufifrons* network (p=0.405 and p=0.097 respectively).

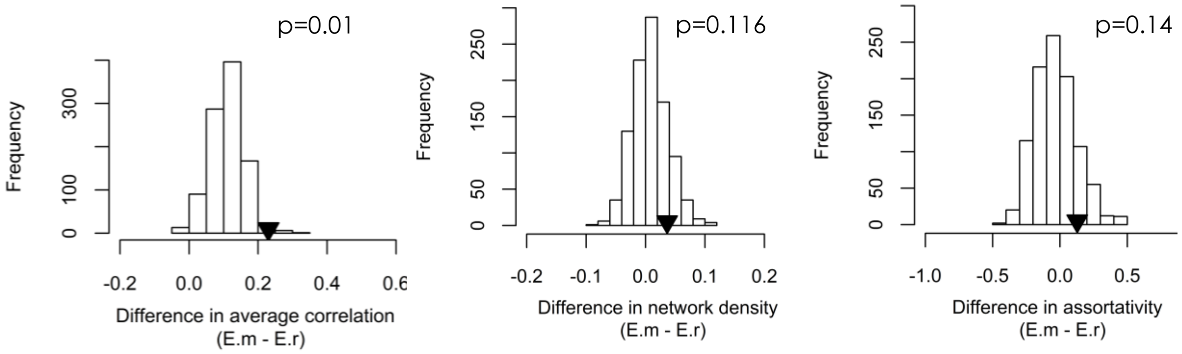


Figure II.8: Differences between the network properties measures of *E. mongoz* and *E. rufifrons* calculated from 1000 null models. The empirical difference values are shown as black triangles. The observed difference in average correlation coefficient is significantly greater than the ones obtain at random (p=0.011) but the differences obtained in network density and assortativity are not different from the one observed at random (p=0.116 and p=0.14 respectively).

4. Number of signal assemblages and combinations

E. mongoz individuals were observed to use 24 different types of assemblages (i.e., signal combined in the 0-1s time frame; Figure II.9.1), while *E. rufifrons* individuals were observed to use 48 different types of assemblages (Figure II.9.2). These numbers correspond to comparable and relatively low values of network density in both species with 0.14 in *E. mongoz* and 0.12 in *E. rufifrons*. Only 3 and 4 assemblage types in *E. mongoz* and *E. rufifrons* respectively occurred with a probability greater than 0.2 (Figure II.9), as shown by the relatively low average probability values of 0.01 in both species. In both species, these assemblages did not seem to occur significantly more often within or between modalities (E.m: 0.43±0.47, p=0.276 and E.r: 0.01±0.05, p=0.933).

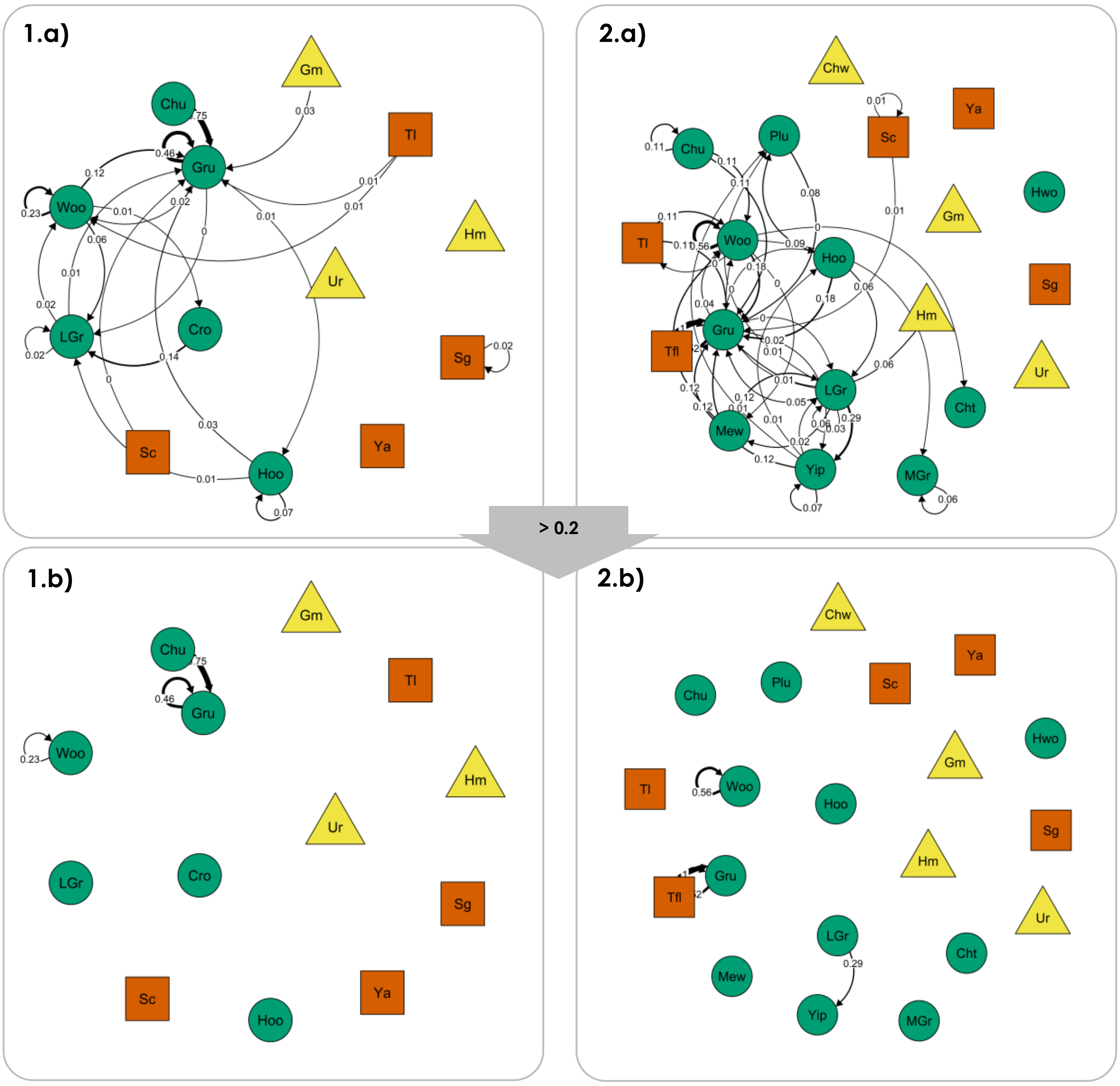


Figure II.9: Network representation of the probabilities of signal assemblages (less than 1s between the two signals are exhibited) for **1.** *E. mongoz* and **2.** *E. rufifrons* with **a)** all possible successions or **b)** only successions occurring with a probability greater than 0.2. Chu=Chuck; Cht=Chutter; Cro=Croack; Gru=Grunt; LGru=Long-grunt; MGr=Modulated-grunt; Hoo=Hoo; Hwo=Hoob-woo; Mew=Mew; Plu=Plurr; Woo=Woof; Yip=Yip; Chw=Chew branch; Gm=Anogenital-mark; Hr=Head-rub; Hrp=Head-rub partner; Ur=Urinate; Tfl=Flick-tongue; Sc=Scratching; Sg=Self-grooming; Tl=Tail-waving; Ya=Yawn

E. mongoz individuals were observed to use 69 different types of sequences (i.e., signal combinations in the 1-60s timeframe; Figure II.10.1), while individuals *E. rufifrons* were observed to use 88 different types of sequences (Figure II.10.2). In *E. mongoz,* this number corresponds to a network density of 0.41, while it represents a network density of only 0.2 in *E. rufifrons*. Only 13 and 18 sequence types in *E. mongoz* and *E. rufifrons* respectively occurred with a probability greater than 0.2 (Figure II.10), as shown by the relatively low average probability values of 0.04 in *E. mongoz* and 0.02 in *E. rufifrons*. In both species, these sequences seem to occur significantly more often within modalities than between modalities (E.m: 0.77±0.09, p<0.001 and E.r: 0.56±0.14, p<0.001).

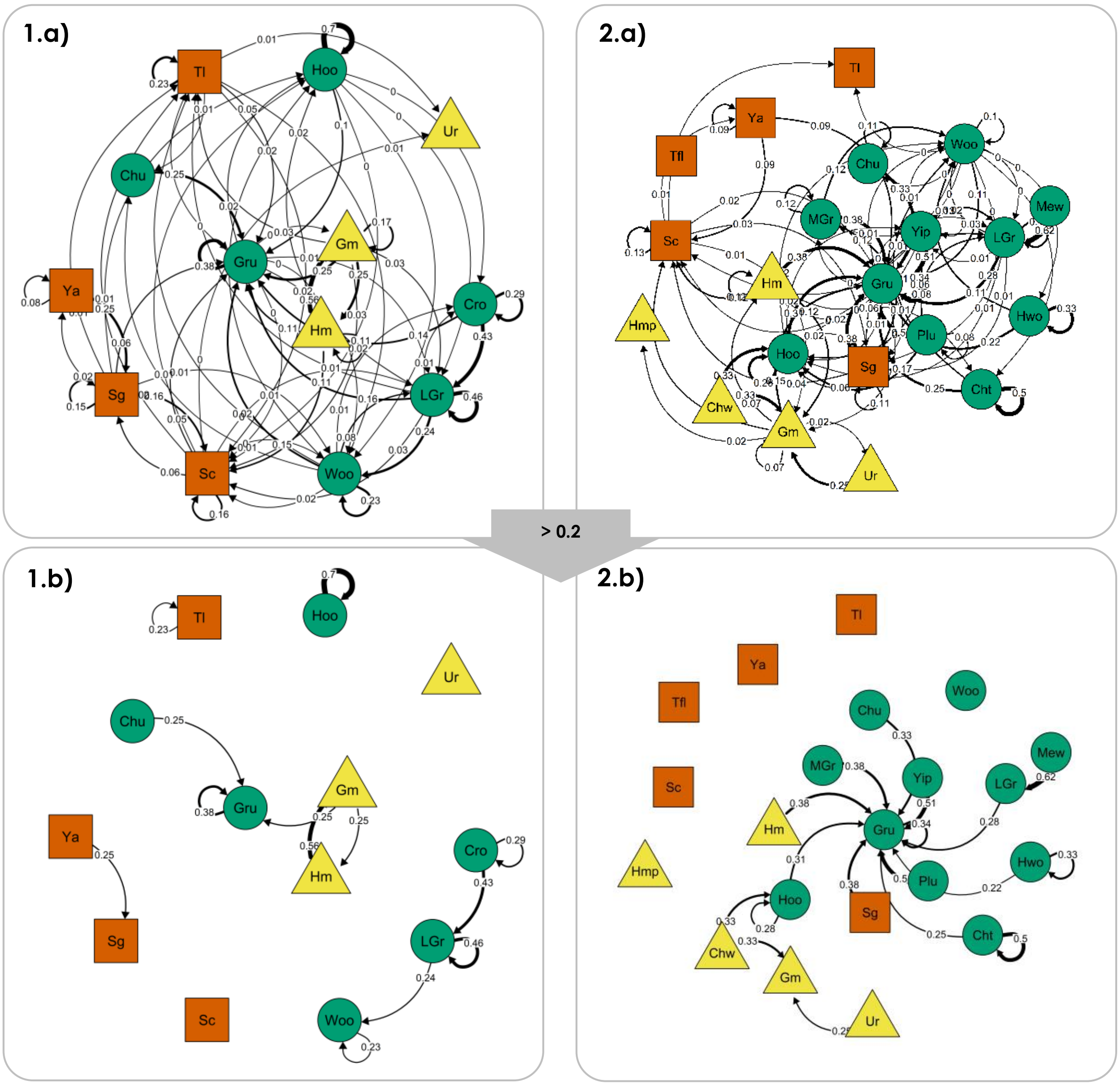


Figure II.10: Network representation of the probabilities of signal sequences (between 1 and 60 seconds between the signals) for **1**. *E. mongoz* and **2.** *E. rufifrons* with **a)** all possible successions or **b)** only successions occurring with a probability greater than 0.2. Chu=Chuck; Cht=Chutter; Cro=Croack; Gru=Grunt; LGru=Long-grunt; MGr=Modulated-grunt; Hoo=Hoo; Hwo=Hoob-woo; Mew=Mew; Plu=Plurr; Woo=Woof; Yip=Yip; Chw=Chew branch; Gm=Anogenital-mark; Hr=Head-rub; Hrp=Head-rub partner; Ur=Urinate; Tfl=Flick-tongue; Sc=Scratching; Sg=Self-grooming; Tl=Tail-waving; Ya=Yawn

IV. Discussion

My general prediction of a more complex communicative system in *E. rufifrons*, the species having a more complex social system (group-living and egalitarian structure) compared to *E. mongoz*, was supported by my results. *E. rufifrons* had larger signaling repertoires (both across and within modalities), greater vocal and olfactory signaling rates, and exhibited a greater number of signal combinations (both in terms of assemblages and sequences). The signaling network of *E. rufifrons* also had a significantly greater degeneracy level (representing more uncertainty in the signals usage) than the one of *E. mongoz*.

Here I first discuss in more detail how the two communicative systems described differ, looking at each measure one after the other and confronting my results with the literature. As I argue that non-homologous signals are especially key for understanding the specific selective pressures at play in the evolution of communicative systems, I further discuss the potential function associated with these non-homologous signals. I then discuss my results regarding possible evolutionary paths at the system level and discuss some potential weaknesses of this species comparison. I finally discuss the advantages and limitations of the proposed framework and its significance at the cross-taxonomic scale.

1. Size of the signaling repertoires

As predicted the signaling repertoire of *E. rufifrons*, the species considered as more socially complex, appear to be larger than the one of *E. mongoz*. The non-homologous signals were all identified in *E. rufifrons* and are mainly signals previously reported to be used in the context of social interactions occurring at the intragroup level. Only the non-homologous olfactory signals observed may rather serve a social function at the intergroup level. These results are in coherence with the idea that *E. rufifrons* may need a greater diversity of signal types to manage their social relationships in larger groups having an egalitarian structure.

We identified 6 acoustic signals in *E. mongoz* and 12 in *E. rufifrons*. Previous literature reported a vocal repertoire of *E. mongoz* ranging from 4 to 15 calls (Tattersall and Sussman 1975; Petter and Charles-Dominique 1979; Curtis and Zaramody 1999; Nadhurou et al. 2015; Gamba et al. 2015) and a vocal repertoire of *E. rufus* (closest sister species of the *E. rufifrons*, these two species being merged until recently; Markolf and Kappeler 2013) ranging between 11 and 18 calls (Pereira and Kappeler 1997; Gamba et al. 2015). The sizes of vocal repertoires reported here are, hence, in the range of previously reported values. In this study, I classified signals based on visual inspection of the spectrogram and did not consider the context of emission as a factor to discriminate between call types, which may explain the differences with other studies. Most importantly, in this study, signal identification was performed with a similar method in both species. I identified 6 acoustic signals in the vocal repertoire of *E. rufifrons*: yip, mew, plurr, hoob-woo, modulated grunts, and chutter, that were not recorded in *E. mongoz*. Five of these calls have been described to be used in intragroup social contexts, at both close and long-range, such as grooming and play interactions or during group movements (Table II.4). Only the chutter call was described to be used in response to the presence of raptors or the context of aggressive intergroup encounters.

We also identified 4 olfactory signals in *E. rufifrons* that we did not observe in *E. mongoz*. These behaviors were bite marking (chew branches), palmar rubbing, anogenital scent-marking of a partner, and head-rubbing of a partner. If the absence of bite marking in *E. mongoz* was already highlighted in a previous comparative study (Colquhoun 2011), these results differ from the ones reported in previous literature, as palmar rubbing, anogenital scent-marking of a partner, and head-rubbing of partner were previously also reported for *E. mongoz* (Harrington 1978; Curtis and Zaramody 1999; Colquhoun 2011). Interestingly, anogenital scent-marking of a partner in *E. mongoz* was described as non-sex specific with both females and males marking their partners while for the group of brown lemurs (including *E. rufifrons*) it was described, in accordance with our observations, as a male-specific behavior. In *E. mongoz* scent-marking behaviors were reported to be mainly associated with intergroup encounters and mating events (Tattersall and Sussman 1975; Colquhoun 2011). A pair-bonding maintenance function of scent-marking has also been shown in the other pair-living true lemur species *Eulemur rubriventer* (Overdorff and Tecot 2006). In this sense, the absence of certain scent-marking behaviors in our observations of *E. mongoz* may be due first to the fact that I choose to observe the individuals outside of the mating season. Differences in the frequency of group encounters between the two species may also contribute to explain these divergences. In *E. mongoz* intergroup encounters are reported to be rare and short (Tattersall and Sussman 1975) and during this study, we did not observe any group encounter between groups of *E. mongoz*. In *E. rufifrons*, on the other hand, we observed regular group encounters during the study period, some lasting for several hours. Moreover, in other lemur species, scent-marking behaviors have also been proposed to serve for intra-sexual communication (Kappeler 1998 in *Lemur catta*; Kraus et al. 1999; Lewis 2005 in *Propithecus verreauxi*; Gould and Overdorff 2002 in *Eulemur rufus*; Pochron et al. 2005 in *Propithecus edwardsi*). Males may use anogenital scent-marking for advertising their social or reproductive status to other males of their group as a form of indirect competition (but see chapter III). This may be an additional function of the scent-marking behaviors we observed in *E. rufifrons* outside the mating season, especially as these non-homologous olfactory signals are male-specific in *E. rufifrons*. Functions of bite marking and palmar rubbing remain unknown. Because bite marking seems to be absent of the signaling repertoire of *E. mongoz* but also the one of the *E. rubriventer*, the only other monogamous species, it may be particularly relevant to study its function (Colquhoun 2011).

Very little is known about the visual communicative signals used by lemurs, yet, several studies on other primate species showed the importance of visual signals in social interactions (Liebal et al. 2004b, a, 2006; Maestripieri 2005). One visual signal was observed only in *E. rufifrons* and never in *E. mongoz*, the flick-tongue behavior. Only one previous study reported this behavior in this species (Pereira and Kappeler 1997) and suggested that it may have a greeting function; however, this function remains speculative. This signal was always observed at the intragroup level and was mainly produced by males (76% of the case; n=46; unpublished data) and in the direction of another individual, in 72% of the cases an individual from the same sex (n=18; unpublished data).

2. Signaling rates

The general call rate (frequency of production of an acoustic signal) and general rate of olfactory signals were both significantly greater in *E. rufifrons* than in *E. mongoz*. However, with the significant exception of the grunt call, the differences between signaling rates in homologous signals seem to be limited and do not seem to be associated with social intragroup communication functions. The difference observed in the anogenital scent-marking rate is likely attributed to a social function at the intergroup level. Differences in the signaling rate of homologous visual signals may rather be attributed to allospecific functions.

When looking at the 5 homologous calls, only the grunt rate significantly differed between the two species. *E. rufifrons* appeared to produce grunts above ten times more often than *E. mongoz*. Grunts were described as contact calls that serve a group cohesion function, especially when the distance between individuals increases during group movement and foraging (Pflüger and Fichtel 2012; Sperber et al. 2017). In *E. rufifrons*, grunts have also been shown to serve a function of regulation of the interactions, as its usage seems to facilitate peaceful outcomes of approach behaviors between partners (Pflüger and Fichtel 2012). If both species are described as highly cohesive, *E. mongoz* seems to remain considerable amounts of time in really close distances, and events of group separation are comparatively rare (personal observations; Tattersall and Sussman 1975). *E. rufifrons* having larger groups, successful cohesion may require more coordination behaviors. Both species live in sympatry with several other lemur species, but only *E. mongoz* live in sympatry with another true lemur species, the *E. fulvus* (Curtis and Zaramody 1998). We observed *E. mongoz* to be particularly silent and immobile in the presence of *E. fulvus*, this difference may also partially contribute to explaining a general decrease in call rate in *E. mongoz*. If the time spent in presence of *E. fulvus* was not quantified over the period of observations, these events remain sparse and the level of activity during our observations was comparable in both species. Both species indeed appeared to be traveling or feeding on average around 17 minutes per hour (E.m: 17.5 ± 1.1 m/h and E. r: 17.1 ± 0.3 m/h). Hence, I believe that this should not have importantly impacted the data reported here.

Concerning the olfactory signals, the general signaling rate was also significantly greater in *E. rufifrons*. However, when looking specifically at the two homologous signals, only the rate of anogenital marking by females was significantly greater in *E. rufifrons* than in *E. mongoz*. Female red-fronted lemurs are philopatric and inherit the territory of their mother, so they may have an especially steep interest in defending their territory and its associated resources. They have indeed been shown to take part in intergroup interactions more often and more aggressively than males (Pyritz 2011). The differences in the frequency of group encounters between the two species mentioned in the precedent section may hence be responsible for this result.

Usage of visual signals such as tail-waving or flick-tongue in these two species were mentioned but never quantitatively described (Tattersall and Sussman 1975; Fichtel and Hammerschmidt 2002). Regarding the visual signals, the picture was more contrasted, indeed while scratch and yawn were more often produced in females *E. rufifrons* than in females *E. mongoz*, tail waving was more often produced by both males and females *E. mongoz*. Tail-waving is associated with the presence of a disturbance; this behavior was indeed observed mainly in the presence of the *E. fulvus* or of a dog that was regularly roaming around the area of one group. Hence, differences in the homologous visual signaling rates may not be attributed to social functions.

3. Degeneracy of the signaling system

As predicted, I found a higher degeneracy of the system in *E. rufifrons* (Figure II.12). In other terms, there was less uncertainty in the system of the *E. mongoz*, meaning that from partial information on the signaling behavior of one individual, we can more reliably predict its behavior regarding other signals. This relationship was significant for the average correlation but not for network density. This means that the proportion of signals for which we can extract information is similar in both species, but the accuracy with which information can be extracted is increased in *E. mongoz*. This can be associated with an overall higher degree of homogeneity and less flexibility in signal usage in *E. mongoz*. This is coherent with the idea that *E. rufifrons* would require greater flexibility in their communicative systems to navigate a more uncertain social environment associated with larger groups and an egalitarian structure.

4. Modularity of the signaling system

E. mongoz appeared to have an assortativity coefficient greater than random, which means that we can better predict the behavior of an individual within than across modalities. For instance, partial information on the vocal activity of an individual would provide more robust information on its behavior regarding other acoustic signals than on its olfactory or visual signaling behaviors. The assortativity coefficient of *E. rufifrons* does not differ from random, meaning that the behavior of an individual cannot be better predicted within or across modalities. Hence, *E. mongoz* tended, as predicted to have greater modularity of their system, but this difference was not significant (Figure II.12).

5. Number of signal assemblages and combinations

The absolute number of combinations (both assemblages and sequences) was as predicted greater in *E. rufifrons* compared to *E. mongoz*. However, the observed number of sequences relative to the possible number of sequences was greater in *E. mongoz* showing that *E. mongoz* may partially compensate their smaller signaling repertoire and assemblage types by increasing the possible sequential associations between these signals. Most of the non-homologous combinations present only in *E. mongoz* were composed of signals used in contexts related to the presence of a disturbance. By contrast, the non-homologous combinations present in *E. rufifrons* associate more often signals used in a social context. Signal combinations occurred more often within than between modalities in both species.

In *E. mongoz*, chuck-grunt assemblages were among the most common assemblages observed. Chuck calls are considered aerial alarm calls. This assemblage also exists in *E. rufifrons* but with a lower probability. Two other most common assemblages in *E. rufifrons* engaged signals that don't have their homolog in *E. mongoz*. Flick tongue was always associated with grunt calls, and long-grunts were often associated with yip calls.

E. mongoz produced, with a high probability, sequences of repeated calls as long-grunts, woof, and croacks, or long-grunt-woof and croack-long-grunt sequences. The three acoustic signals being involved in these sequences being produced in the context of the presence of a disturbance. *E. mongoz* also more often repeated the tail-waving behavior that is also produced in the presence of a disturbance. In *E. rufifrons*, chutter and hoob-woo calls were also often repeated. If the chutter is also used in the context of disturbances, hoob-woos are social calls associated with grooming interactions or approaches. In *E. rufifrons*, most of the social calls (hoo, modulated grunt, yip, long-grunt, plurr, hoob-woo) were often followed by grunts.

6. Are we sure of what we compare?

Given the presence of intraspecific variation in social organization (Agnani et al. 2018; Schradin et al. 2018), one could argue that rather than comparing two species, I compared two populations. If this is uncontestably an important concern to raise, previous studies in true lemurs report relative stability of social systems across populations and groups (Kappeler and Fichtel 2015). I then expect the variation to be smaller across populations than across species. This may not be true anymore when *E. mongoz* are forced to form larger groups due to habitat fragmentation (chapter IV). A perspective here would be to characterize the social system of these two populations and to relate signal usage to specific social variables. Detailed comparative studies on a restricted number of closely related species allow taking a closer look at how sociality has driven the evolution of communication by limiting the effect of alternative hypotheses (Gustison et al. 2012; Bouchet et al. 2013; Peckre et al. 2019).

If I put special effort in choosing two closely related species having an ecology and morphology as similar as possible, few differences (besides the ones associated with their social systems) persist, and I tried to discuss most of them in the preceding paragraphs. However, another important difference in the populations we studied that was not addressed yet is their level of habituation. If the population of *E. rufifrons* has been studied for twenty years, as far as I know, the population of *E. mongoz* was not subject to any long-term study. If I cannot exclude an effect of our presence, I believe that this effect is relatively limited. First, if some disturbance behaviors occurred during the first encounters, these behaviors rapidly cease. As we only started observations on a group 2-4 days after first encountering them as we needed to be sure of individual identity, these behaviors were not included in our observations. Moreover, as mentioned earlier, the level of activity was comparable in both species; hence, I also believe that the *E. mongoz* we observed did not refrain from their usual activity.

Finally, here I chose to study their communication systems outside of the mating and birth season. This schedule may be why we missed observing some behaviors previously reported in the literature. To characterize the full signaling system of a species, it may be necessary to study this behavior across the entire year. However, here I have put special effort into studying both species in equivalent social seasons allowing a meaningful comparison. As a perspective, comparing the signaling network of these species between different seasons may also be relevant to identify the function of the different signals.

7. The global picture

To sum up, I observed an increased signal diversity in the repertoire of *E. rufifrons* compared to the one of *E. mongoz* with 11 non-homologous signals whereof at least 6 (5 acoustic and 1 visual) are used in a social context at the intragroup level. Additionally, 4 olfactory signals were found to be non-homologous (at least during the season studied) and have likely a social function at the intra or intergroup level. These signals: yip, mew, plurr, hoob-woo, modulated grunts, flick tongue, anogenital scent-marking of a partner, head-rubbing of a partner, palmar rubbing, and bite marking are particularly interesting candidates for further studies on their social function revealed by my analyses (Blue 2020). Increased signaling rates were also observed in *E. rufifrons* compared to *E. mongoz* for the acoustic and olfactory modalities. These differences were explained by increased signaling rates associated with both homologous (i.e., grunt) and non-homologous (i.e., flick tongue) signals. The only signal found to be more often produced by *E. mongoz* than by *E. rufifrons*, the tail-waving, was produced in allospecific contexts (i.e., presence of a disturbance). *E. rufifrons* were also observed to express greater number of possible signal combinations (both assemblages and sequences). Most of the non-homologous combinations present only in *E. mongoz* were composed of signals used in contexts related to the presence of a disturbance. By contrast, the non-homologous combinations present in *E. rufifrons* associate more often signals used in a social context. A higher level of degeneracy was also found in the communicative system of *E. rufifrons* compared to the one of *E. mongoz*. Hence, *E. rufifrons*, the species having the more complex social system, also had overall a more complex communicative system than the one of the *E. mongoz*. Both, careful choice of the species compared to limit the effect of possible additional selective pressures, and exploration of the social function of the non-homologous signals allow me to conclude that this increased complexity of the communicative system in *E. rufifrons* is most likely associated with social selective pressures.

8. Insight on possible evolutionary paths

Multimale-multifemale groups exhibiting female dominance appear to be the ancestral state in true lemurs (Petty and Drea 2015; Kappeler and Fichtel 2015; Figure II.11). Indeed, the genus "*Eulemur*" constitutes one of the rare cases of a probable transition from a group living ancestor to social monogamy in mammals (Lukas and Clutton-Brock 2013; Kappeler and Fichtel 2015). This has several implications for the interpretation of my results. First, the social systems of both species could have incurred changes from the putative ancestral state, albeit in different social dimensions and different directions. While *E. rufifrons* would represent an increased social complexity through the evolution of an egalitarian social structure from a female dominance ancestor, *E. mongoz* would have reduced its social organization complexity by transitioning to social monogamy from a group living ancestor. Second, these social changes interpreted under the SCHCC could imply that the observed differences are derived from 1) increased communication complexity in *E. rufifrons* compared to the ancestral state, 2) reduced communicative complexity in *E. mongoz* compared to the ancestral state or 3) a combination of both. In scenario 1), my results should be interpreted as showing evidence for the SCHCC with the communicative system of *E. rufifrons* having been complexified as a result of complexifications in the social system. Scenario 2) on the contrary suggests the possibility of enlarging the SCHCC to include also the possibility of simplification of communicative systems as a result of the evolution of less complex social systems. Even more interesting, scenario 3) could offer the possibility of comparing the evolutionary forces of complexification and simplification of communication systems in response to social systems against each other to assess differences in the plasticity of these traits depending on the directionality of selection. Despite the interest of such scenarios for discussing the SCHCC, the current knowledge on the social (Figure II.11) and communicative systems of true lemur species are still incomplete precluding such paths of investigation. Nevertheless, I think that these ideas together with the proposed framework for investigating communicative complexity open up new interesting areas of research, that could provide in the future, together with detailed knowledge on other species traits and their phylogenetic relationships, a deeper understanding of the evolution of communication in animals.

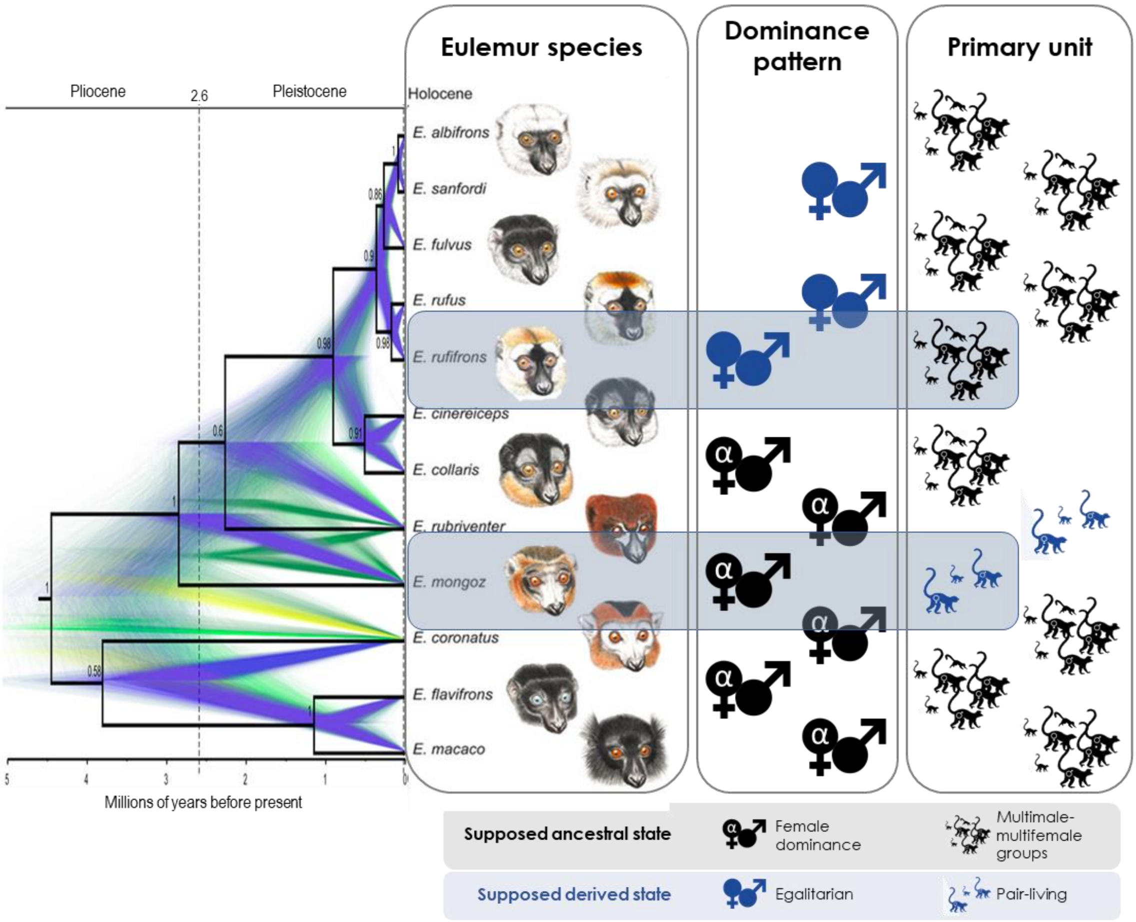


Figure II.11: Time-calibrated species tree of the genus *Eulemur* and the associated dominance and primary unit patterns of the 12 species. This figure is based on a figure published by (Markolf and Kappeler 2013)

9. Our approach: advantages and limits

In this study, I attempt to provide a framework of operational measures to quantify the complexity of a communicative system across different dimensions. I first argue that the number of signals, signaling rates, and the number of signal combinations are relevant measures that can be applied across modalities and taxa. I then extend this framework to the measure of degeneracy and modularity of the signaling system based on the field of phenotypic integration. The measure of degeneracy provides us with information on the level of certainty (or uncertainty) with which we can predict the signaling behavior of an individual belonging to this system from only partial information. If the degeneracy level informs us about the level of predictability across the whole signaling system, the level of modularity informs us about whether this level of certainty is more pronounced within or between signaling modalities. In Figure II.12, I provide a visual illustration of the three-dimensional space of communicative complexity defined by the three signaling network property measures used in this study. I place *E. rufifrons* and *E. mongoz* in this space and provide toy examples of network representations that could be observed in each area of this space.

When degeneracy increases, the level of uncertainty in the system increases. In societies where the signaling behavior of an individual is strictly determined by its caste, age class, sex, or dominance status, the level of degeneracy is expected to decrease (more and stronger correlations between signals) when the number of classes increases. Moreover, the lower the variability between individuals within these classes is, the more predictable the system becomes (i.e., the level of degeneracy of the system decreases). However, the more these different social classes will overlap on the number of signals they use, the more the degeneracy will increase. On the contrary, in societies where all individuals use all or many of the signals available at the species level, and in more flexible ways across and within contexts, the level of degeneracy of the system is expected to increase drastically. It is also important to note that the time scale considered is highly relevant. If individuals are susceptible to change status across their lifetime, this will also impact the aspect of the network. A network may be highly integrated at a certain scale and become degenerated at a larger time scale when individuals take different roles over time.

In my framework the edges of the networks represent both positive and negative correlations between the rate of usage of different signals, therefore, one should not conclude about a decreased degeneracy that individuals using one signal will also use more all the other signals. Instead, decreased degeneracy would imply that from one signal, we can predict the signaling activity on many other different signals in the system (increased network density) with higher reliability (increased correlation).

The level of modularity informs us about whether the predictability measured using degeneracy is more pronounced within or between signaling modalities. Similarly, I consider absolute correlation values implying that one should not conclude based on a high value of assortativity (close to 1) that individuals that use more the signals from one modality would also use more another signal from the same modality, but rather that we can better predict the behavior within modalities than across modalities.

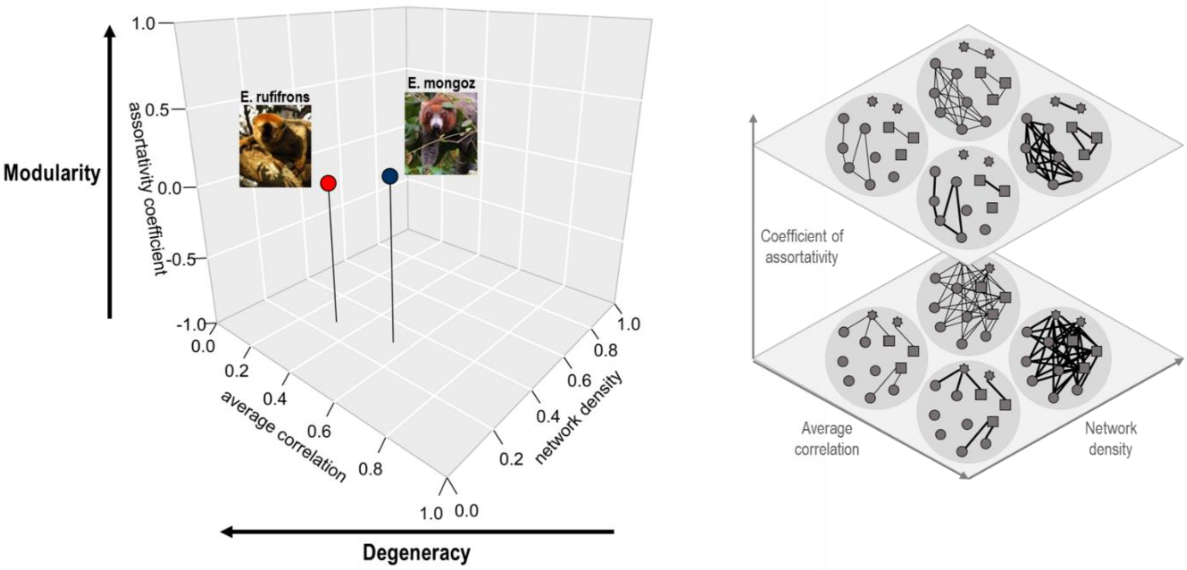


Figure II.12: position of *E. mongoz* and *E. rufifrons* in the three-dimensional space of communicative complexity defined by the three signaling network property measures used in this study and illustrative description of the network space

The framework I propose here is intended to describe the level of complexity at the signaling system level, but as I see, these measures also reflect the level of complexity faced by the individuals. I hence hope to provide a more comprehensive description of the complexity of a signaling system. However, I believe that my approach finds its main limitations in the fact that the measures offered rely on an objective assessment of the different signals. Difficulties in assessing the signaling repertoire may arise from both variations in the definition of signals or variations in sampling methods (Molesti et al. 2019). Hence an effort of consistency is needed to provide a solid comparison basis of the signaling repertoire across species.

Three main issues may result in the omission of relevant signals: first, depending on the level of definition chosen a signal may not be considered as such. Second, alternative sampling methods may differ in their sensitivity to rare signals. Finally, some modalities may be harder to detect due to our inherent human bias. Traditionally, the field of animal communication has made a distinction between signals that are generated to provide information to another animal and cues that are generated either inadvertently or for a purpose different than communicating information. However, many actions performed by animals cannot be easily assigned to one of these discrete categories but may have both signaling and non-signaling functions (Bradbury and Vehrencamp 2011). Hence here I based my signal classification on a broad and raw sense of the term signal including both signals and cues. To avoid circularity between sociality and communication, I first, distinguished signals based on their structure and not on their context of emission and chose not to include behaviors that are usually considered to assess social relationships such as grooming, body contact, approaches, or aggressions (Peckre et al. 2019). A second issue relates to the sampling effort; if some species produce much of the diversity of their signaling repertoire in a short timescale, others need much larger time scales (e.g., seasonal behavior, rare behaviors, etc.). Usually, a comprehensive estimation is difficult, but some methods exist to assess the reliability of sampling (see for instance Kershenbaum et al. 2015). Finally, some signals may be omitted because we do not perceive them or need technology to perceive them. As McShea pointed out with humor, “if a cat seems to have more parts than a clam it could just be that it is larger, with parts that are easier to see and that are also more familiar to us” (McShea 1991). Infra- and ultrasound, infrared radiation, ultraviolet reflection, electric fields, or cryptic olfactory behavior may particularly be overlooked (Prat 2019). This leads us to an additional issue when classifying signals in distinct modalities based on the primary sensory channel involved. In reality, single signals usually involve multiple modalities simultaneously (Partan and Marler 1999). One potential solution would be to attribute different modalities to each signal and to provide a range of assortativity values rather than a unique value. For instance, scent-marking behaviors can be considered simultaneously as olfactory and visual signals (chapter III). Thus, to limit the impact of attributing it to either modality as I did in my analyses, a solution would be to rerun the analyses of modularity and degeneracy with each possibility. In the case of a species with one scent-marking signal, one network including it as olfactory and another as visual should be used for analyses. If this is implemented in a species with several multimodal signals, all combinations of assigned modalities should be used and a range of values of assortativity and modularity recovered. This would reduce the reliability of measures but comparisons of species and their range of values could still be possible.

V. Conclusion

In summary, I first hope to have highlighted the importance of looking at specific differences in the communicative system of closely related species having different social systems to reveal the signals of interest and to explore how specific sociality aspects may have led to the emergence or disappearance of specific signals (Gustison et al. 2012, 2019; Bouchet et al. 2013; Molesti et al. 2019). *E. rufifrons*, the species having the more complex social system, also had overall a more complex communicative system than the one of the *E. mongoz*. Both careful choices of the species compared to limit the effect of possible additional selective pressures and exploration of the social function of the non-homologous signals allow concluding that this increased complexity of the communicative system in *E. rufifrons* is most likely associated with social selective pressures.

Second, I described a new analytical framework to assess the complexity of signaling systems across modalities. I developed this framework with the perspective of facilitating cross-taxonomic comparisons. My approach remains tentative, and I encourage other researchers to apply this framework to additional species. First, this would help to resolve several of the current limits pointed out in the discussion and would allow us to gain a greater understanding of the evolutionary significance of degeneracy and modularity of a communicative system. In particular, my approach may be combined with new multi-dimensional approaches of social complexity (Kappeler 2019; Hobson et al. 2019; Prox and Farine 2020) and contribute to a more holistic approach to the tests of the SCHCC. By this, we should be able to derive new testable hypotheses that would contribute to better understand the course of events that have led to the evolution of communication diversity in its distinct dimensions (Waller et al. 2013).

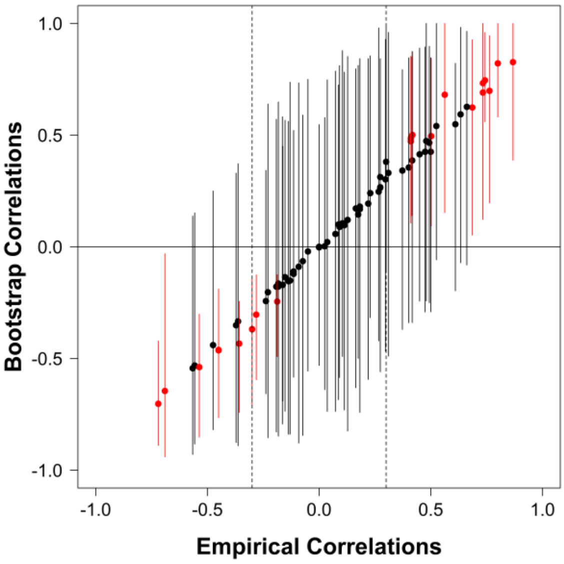
VI. Acknowledgments

I am most thankful to Lluís Socias Martínez for his careful review and critics on a first version of this manuscript. I thank the Malagasy Ministère de l'Environnement et des Eaux et Forêts, the Direction Générale de l'Environnement, de l'Ecologie et des Forêts de la région de Boeny, the Département de Biologie Animale of Antananarivo University, and the Centre National de Formation, d'Etudes et de Recherche en Environnement et Foresterie for supporting and authorizing my research. For data collection on mongoz lemurs, I warmly acknowledge Basile Andriambeloson, Janoarisaona Randrihaniharisoa, Armand-Célestin Tsimanihitra, Lydia Raharisoa, Mônique Rayanadramiasy and Lilas Allard for their guidance and participation in data collection. I also thank the VOI members of Mariarano village, the DBCAM (Development and Biodiversity Conservation Action for Madagascar) members, and Rodin Rasoloarison for their contribution to implementing the research site. For data collection on red-fronted lemurs, I am most grateful to Charlotte Defolie, Julia Penndorf, Patrick Solondrainy and Mamy Razafindrasamba for their contribution. This study was funded by the Deutsche Forschungsgemeinschaft (DFG FI 929/13-1) (DFG FI 929/21-1) and the German Primate Center. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

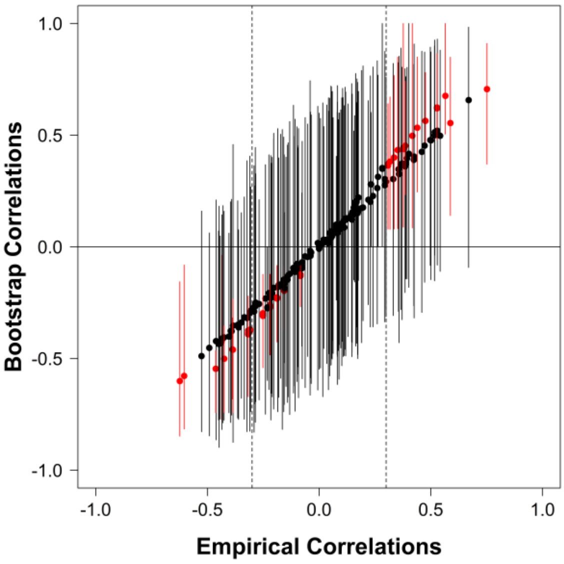
VII. Supplementary material

Supplementary Table II.1: Description of the social system of the mongoose lemurs (*E. mongoz*) and red-fronted lemurs (*E. rufifrons*). Social parameters are based on Kappeler 2019; Prox and Farine 2020.

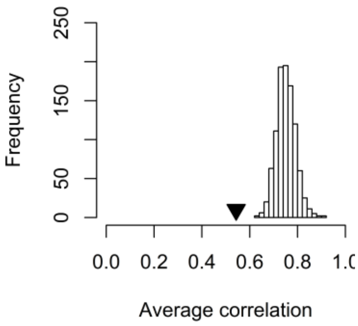
	Parameter/ variable	**Mongoose lemur (*E. mongoz*)**	**Red-fronted lemurs (*E. rufifrons*)**
Social organization	Primary Unit or Pattern	Pair/Family (Kappeler and Fichtel 2015)	Group (Kappeler and Fichtel 2015)
	Group size	2.8 ± 0.8 individuals Pair to small (Kappeler and Fichtel 2015)	5.4 ± 2.3 individuals Small to large (Kappeler and Fichtel 2015)
	Group composition	Family group: one adult pair and their immature offspring (two generations) (Tattersall and Sussman 1975; Kappeler and Fichtel 2015)	Two adult females, four adult males, two juvenile females, and one juvenile male (Kappeler and Fichtel 2015)
	Adult sex ratio	multimale/multifemale 1:1 (Tattersall and Sussman 1975; Kappeler and Fichtel 2015)	multimale/multifemale 1:1 to 1:2 (F:M) (Ostner and Kappeler 2004; Kappeler and Fichtel 2015)
	Kinship pattern	Pair (Tattersall and Sussman 1975)	Matriline (Ostner and Kappeler 1999; Kappeler and Port 2008)
	Offspring membership	Extended (Tattersall and Sussman 1975)	Extended (males) & Philopatric (females) (Kappeler and Fichtel 2015)
	Temporal stability	Long-lasting to permanent	Long-lasting
Social structure	Dominance hierarchy - Tolerance	Female dominance (Curtis and Zaramody 1999)	No linear dominance hierarchy nor one sex consistently dominant over the other but one central male (Pereira et al. 1990; Ostner and Kappeler 2004; Fichtel et al. 2017)
	Cohesiveness	Very cohesive (Tattersall and Sussman 1975)	Cohesive (Pyritz 2011; Sperber et al. 2019)
	Grooming reciprocity	Grooming relatively infrequent (Tattersall and Sussman 1975)	(Port et al. 2009)
	Intergroup interactions	Rare, short and aggressive (Tattersall and Sussman 1975)	Regular, long, passive or aggressive (Pyritz 2011)
Mating system	Mating pattern	Monogamous (Kappeler and Fichtel 2015)	Polygynandrous (Kappeler and Fichtel 2015)
	Reproductive skew	?	71% of infants sired by dominant male (n=38) (Kappeler and Port 2008)
	Seasonality	Seasonal (Tattersall and Sussman 1975)	Seasonal (Ostner and Kappeler 1999)
Care system	Parental care	Maternal	Maternal
	Allo-parental care	Males occasionally carry the young (Curtis and Zaramody 1999)	Males and other females may carry the young, other females may nurse (personal observations)



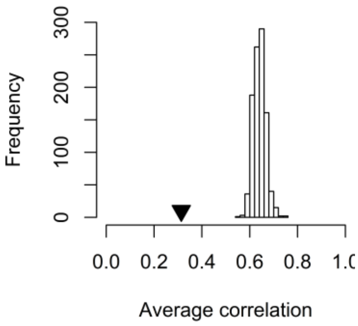
Supplementary Figure II.1: Range of values obtained for each correlation between two signals of E. mongoz during the bootstrapping process (n=1000 iterations). Correlations depicted in red are the ones for which the confidence interval does not overlap with zero, so the one conserved in the final network.



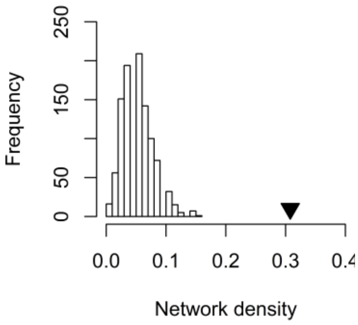
Supplementary Figure II.2: Range of values obtained for each correlation between two signals of E. rufifrons during the bootstrapping process (n=1000 iterations). Correlations depicted in red are the ones for which the confidence interval does not overlap with zero, so the one conserved in the final network.



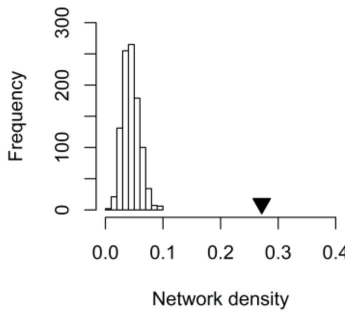
Supplementary Figure II.3: Average correlation values calculated from 1000 null models of the signaling system network of E. mongoz. The empirical value is shown as a black triangle. The observed average correlation coefficient is significantly lower than the randomized values (p≤ 0.001)



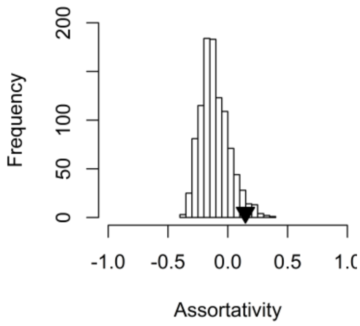
Supplementary Figure II.4: Average correlation values calculated from 1000 null models of the signaling system network of E. rufifrons. The empirical value is shown as a black triangle. The observed average correlation coefficient is significantly lower than the randomized values (p≤ 0.001)



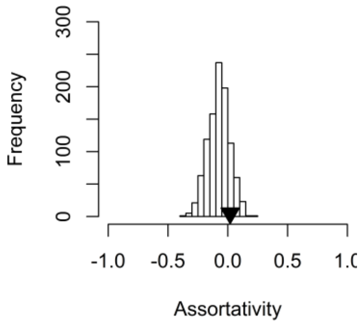
Supplementary Figure II.5: Network density values calculated from 1000 null models of the signaling system network of E. mongoz. The empirical value is shown as a black triangle. The observed network density value is significantly greater than the randomized values (p≤ 0.001)



Supplementary Figure II.6: Network density values calculated from 1000 null models of the signaling system network of E. rufifrons. The empirical value is shown as a black triangle. The observed network density value is significantly greater than the randomized values (p≤ 0.001)



Supplementary Figure II.7: Assortativity values calculated from 1000 random node permutations of the signaling system network of E. mongoz. The empirical value is shown as a black triangle. The observed assortativity coefficient (0.15 ± 0.16) is significantly greater than the node permuted values (p= 0.036), indicating higher assortativity within modalities than the random expectation.



Supplementary Figure II.8: Assortativity values calculated from 1000 random node permutations of the signaling system network of E. rufifrons. The empirical value is shown as a black triangle. The observed assortativity coefficient (0.02 ± 0.08) is not significantly greater or lower than the node permuted values (p= 0.144)

Chapter III: Sex differences in the audience effect on anogenital scent-marking in an egalitarian species of lemur, the red-fronted lemur

With Alexandra Michiels[1,3], Lluis Socias Martinez[1], Peter M. Kappeler[1, 4]& Claudia Fichtel[1,2]

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Contributions (following CRediT taxonomy): Conceptualization, L.R.P., C.F, and P.M.K.; Methodology, L.R.P., L.S.M, and C.F.; Formal analysis, L.R.P.; Investigation, L.R.P., A.M.; Resources, L.R.P., C.F and P.M.K.; Writing – original draft preparation, L.R.P.; Writing – review and editing, L.R.P, L.S.M., A.M., and C.F.; Visualization, L.R.P.; Supervision, C.F., and P.M.K.; Funding acquisition, L.R.P., C.F, and P.M.K.

Abstract: Scent deposition is often associated with conspicuous visual displays that may serve to attract the individuals present in the vicinity but may also attract unwanted receivers. Hence, multimodal signals should be flexibly adjusted to the respective audience. Studying the flexibility in usage of a multimodal signal across different audience compositions contributes to uncovering social characteristics that may elicit or constrain complex signal expression. Functional sex differences of scent-marking are common in lemurs. However, to date, the pattern of functional sex differences remains unstudied in egalitarian species. I studied intragroup audience effects in wild red-fronted lemurs. I found an intragroup audience effect in males but not in females. Males deposited less often anogenital marks when more males were present within a three meters range compared to five- or ten-meters ranges. Males may prefer to reduce the risk of physical contact by avoiding to scent-mark near other males, and/or give priority to other males to scent-mark. With these results, I provide important insights into the functional significance of anogenital scent-marking in red-fronted lemurs and support the idea of greater intragroup social pressures associated with anogenital scent-marking in males than in females in egalitarian species.

I. Introduction

Scent-marking behaviors are defined as the deposition by an animal of scented secretion or excretion (e.g., urine, saliva, anogenital secretions) on objects of its environment (Bowen and Cowan 1980; Barrette and Messier 1980). Scent-marking behaviors are widespread in mammals, and their most common forms are spraying urine and rubbing body parts on substrates. These signals can carry reliable information on the age, sex, reproductive and social status of the sender (Brown and Macdonald 1985; Epple 1986; Harris et al. 2018). Since scent signals are long-lasting, remaining in the environment long after the sender left the location, they, on the one hand, allow senders to address these signals to potential receivers at a distance avoiding possible direct responses such as aggression. On the other hand, this particularity exposes senders to uncertainty about the identity of the receivers.

However, scent-marks are often, when deposited, associated with conspicuous ephemeral visual displays conferring to the signal a multimodal nature. These visual components might attract the attention of individuals present in the vicinity, and guide them to the olfactory component of the signal, allowing some regulation on the receivers' identity. Hence, this multimodal nature may confer to scent-marking behavior the capacity to be addressed both to a future audience and the individuals present during deposition (Duvall et al. 1987; Johnston 2005).

The idea that the visual signal of scent-marking behavior may contribute to addressing the present audience was formalized twice. First, the "demonstrative marking hypothesis" was formulated in territorial male Thomson's gazelles that associate urine-feces deposition with an extreme body posture display (Hediger 1949; Walther 1964; Estes 1967). Later the same idea was described as "composite effect" in ring-tailed lemurs (*Lemur catta*) that can either urinate with the tail only slightly raised or combine urine-marking with a conspicuous visual signal, the erection of their tail in the air, attracting the visual attention of receivers to the location of the urine deposit (Palagi and Norscia 2009). This multimodal signal associating urine-marking and tail erection elicited more investigations of group members than when urine was deposited without tail display.

If the multimodal nature of a signal may effectively optimize its transmission by attracting more receivers, it may also attract the attention of unwanted receivers. Hence, to balance these benefits and costs, multimodal signals should be associated with some behavioral flexibility linked with an audience effect. The audience effect is defined as a change in signaling behavior caused by the presence of the audience; where the audience refers to any individual that is within the signal range (Marler et al. 1986; McGregor and Dabelsteen 1996). Multimodal signals have been classified as either fluid or fixed signals (Partan and Marler 2005). In fluid signals, each component (e.g., urine deposition and tail display) may be produced separately. In contrast, signals are fixed when their components are necessarily combined due to the mechanics of signal production (e.g., gland rubbing and anogenital scent deposition). While fluid signals allow variation in signal structure across contexts (e.g., urination with the erected tail, or without tail display), fixed signals only allow variation in usage (e.g., fewer occurrences of the signal when unwanted receivers are in proximity). Audience effects can, hence, refer to both variations of signal structure or signal occurrence depending on the audience composition.

Studying the flexibility of complex signal usage (e.g., occurrence or structural modifications) across social contexts (audience compositions) contributes to uncovering the particular social characteristics eliciting or constraining complex signal expression (Peckre et al. 2019). These social characteristics may in turn constitute social pressures acting for or against the evolution of complex signaling behaviors. However, how social factors directly affect variation in signaling has only rarely been studied, failing to uncover both the specific attributes of communication that would evolve in response to specific aspects of sociality and the actual way how social factors may influence signaling behavior (Pollard and Blumstein 2012; Gustison et al. 2012, 2019; Peckre et al. 2019).

Unlike anthropoid primates, strepsirrhines, a monophyletic group of primates that represent early primates (Yoder 2007) have like most other mammals a functional vomeronasal organ. Strepsirrhine primates rely heavily on olfactory communication and exhibit a wide variety of chemical signals (saliva, urine, feces, and secretions) expressed by glands in various body areas (head, neck, chest, forelimb, and anogenital area; (Schilling 1979; delBarco-Trillo and Drea 2014). Interestingly, in this macroscopic group, diversification of means of olfactory communication went along with broad diversification of ecology, morphology, and social systems, making them excellent models for comparative studies.

Sex differences in the glandular structure and the frequency of scent-marking behaviors are common in strepsirrhines as in other mammals (Jolly 1966b; Mertl 1977; Epple 1986; Gould and Overdorff 2002; Vasey 2003; Pochron et al. 2005; delBarco-Trillo and Drea 2014; Janda et al. 2019). According to sexual selection theory, males should have evolved more complex signals than females. However, strepsirrhines are also characterized by an unusual level of female "masculinization" exhibited by numerous species with social dominance of females over males and particular female features (delBarco-Trillo et al. 2012; Petty and Drea 2015), and a reversed pattern of the traditional sex differences in olfactory cues has even been documented in some female-dominant species (delBarco-Trillo et al. 2012).

Among lemurs, *the* true lemur *clade* (Eulemur, Lemuridae) contains few exceptional species in which both sexes are codominant (*E. sanfordi*, *E. collaris*, *E. rufus,* and *E. rufifrons*). In these group-living egalitarian species, both sexes exhibit conspicuous anogenital scent-marking displays, and even though females seem to have more elaborated glandular folds, the chemical richness of genital secretions is higher in males than in females (delBarco-Trillo et al. 2012). These morphological and physiological differences may be indicative of functional differences. Whereas different functions of scent-marks between sexes have been described for female-dominant lemur species such as ring-tailed lemurs (Scordato and Drea 2007) and Verreaux sifakas (Lewis 2005, 2006), but also in other primate species with male dominance such as mandrills (Vaglio et al. 2015), the pattern of functional sex differences remains unstudied in egalitarian species.

Moreover, most of these studies on the function of scent-marking were carried out on captive animals and looked at inspection and overmarking events. In the wild, however, this approach is complicated by the fact that the nature of the scent is difficult to control. Multiple individuals may have marked the spot in the past, and the information inspected or overmarked may be unclear. One alternative way to explore these functions and potential sex differences is to test for inter and intra-sexual audience effect on scent-marking behaviors in both sexes.

In this study, I examined intragroup audience effects in wild red-fronted lemurs. Red-fronted lemurs live in highly cohesive small multi-female–multi-male groups of 5-12 individuals with an even or male-biased sex ratio (Pereira and Kappeler 1997; Overdorff 1998; Wimmer and Kappeler 2002; Ostner and Kappeler 2004; Sperber et al. 2019). Red-fronted lemurs exhibit a relatively egalitarian social structure with none of the sexes being consistently dominant over the other (Pereira et al. 1990; Ostner and Kappeler 1999).

In lemurs, scent-marking signals have first been suggested to serve a pair-bonding maintenance function, as shown in both pair-living (Overdorff and Tecot 2006; *Eulemur rubriventer*) and group-living species (Greene and Drea 2014; *Propithecus coquereli*). Red-fronted lemurs being promiscuous, with all females mating with virtually all males within their group (Pereira and McGlynn 1997), and no strong male-female bonds being observed

(Ostner and Kappeler 1999) this pair-bonding maintenance function of scent-marking is unlikely. Nevertheless, scent-marking signals have also been suggested to be directed to the opposite sex as a form of mate attraction. If a form of mate attraction takes place, I would expect one sex to increase its probability to anogenital mark in the presence of an increased proportion of individuals of the opposite sex. On the one hand, male red-fronted lemurs seem unable to identify the fertile period of a female, as shown by a prolonged mating period largely exceeding the 1 to 3 female fertile days (Ostner and Kappeler 1999), the reproductive status signaling function seems doubtful in female red-fronted lemurs. On the other hand, because some reproductive skew exists among male red-fronted lemurs (Wimmer and Kappeler 2002; Kappeler and Port 2008), some mechanisms of female mate choice seem to occur. Hence males may be expected to perform more anogenital scent-marking in the presence of an increased proportion of females.

Moreover, scent-marking behaviors have also been proposed to serve for intra-sexual communication. Males may use anogenital scent-marking for advertising their social/reproductive status to other males of their group as a form of indirect competition (Kappeler 1998 in *Lemur catta*; Kraus et al. 1999; Lewis 2005 in *Propithecus verreauxi*; Gould and Overdorff 2002 in *Eulemur rufus*; Pochron et al. 2005 in *Propithecus edwardsi*). Indeed, scent-marking behaviors have more broadly been suggested to be non-overtly agonistic indicators of dominance and are, as such, expected to be more prominent in species with low aggression rates (Epple 1986; Erhart and Overdorff 2008). If there is no linear hierarchy and low aggression levels in male red-fronted lemurs, one central male seems nevertheless to be associating more strongly with all females (Ostner and Kappeler 1999). These central males have besides been shown to scent-mark more than any other males in the group (Ostner and Kappeler 1999). In this way, central males are especially suspected to exert a role of behavioral reduction of reproductive function in subordinate males (Ostner and Kappeler 1999; Gould and Overdorff 2002). For instance, subordinate males may suppress their reproduction to avoid the costs of aggression, including potential evictions (Stockley et al. 2013). In red-fronted lemurs, if most of the males are observed mating, central males have been shown to sire around 60-70% of all infants (Wimmer and Kappeler 2002; Kappeler and Port 2008). Hence, if males use anogenital scent-marking behavior for indirect competition, I predict that male red-fronted lemurs may modify their scent-marking behavior in response to the male audience.

Finally, as in red-fronted lemurs, there is no dominance pattern among females the social status signaling function seems to be unlikely for females. Moreover, competition in females was shown to appear only from a critical group size of about ten individuals

(Kappeler and Fichtel 2012). Hence, due to this low competition level between females, contrary to what we may predict for males, I do not expect to find a female-female audience effect linked to an indirect competition. However, females have also been suggested to use scent-marking to give information to other females about their reproductive status. Indeed, odor communication between females may help them to reduce or increase estrus synchrony. Females ring-tailed lemurs have, for instance, been shown to benefit from estrus asynchrony by maximizing their ability to exercise mate choice (Pereira 1991). In red-fronted lemurs female estrus synchrony seems to occur (Ostner and Kappeler 2004), scent-marking behaviors may also mediate this synchronization. Estrus synchrony may be beneficial in red-fronted lemurs by making it difficult for males to monopolize them. Hence, we may expect a female-female audience effect with more anogenital scent-marking by females occurring in the presence of other females.

Hence, to sum up, considering the social system of red-fronted lemurs I predicted three possible intragroup audience effects: 1) Scent-marking in males may function as a form of mate attraction with males anogenital scent-marking more in the presence of an increased proportion of females. 2) In males, anogenital scent-marking behavior may serve an indirect competition function, males being expected to modify their probability of scent-marking depending on the males present in the audience. 3) Females may optimize their reproduction by synchronizing their estrus; if this synchronization is mediated by anogenital scent-marking, females are expected to anogenital scent-mark more in the presence of an increased proportion of females.

II. Material and methods

1. Study Site and Subjects

We conducted this study in Kirindy Forest, a dry deciduous forest located ca. 60 km north of Morondava, western Madagascar, managed within a forestry concession operated by the Centre National de Formation, d'Etudes et de Recherche en Environnement et Foresterie (CNFEREF). Since 1996, all members of a local population of red-fronted lemurs inhabiting a 70-ha study area within the forest have been regularly captured, marked with individual nylon or radio collars, and subjected to regular censuses and behavioral observations. A grid system of foot trails with intersections every 25 m or 50 m features this area. The data presented in this study were collected from May to November 2018 on 28 adult individuals (11 females and 17 males) belonging to four groups. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The habitat is characterized by pronounced seasonality with a hot, rainy season between November and March and a colder dry season between April and October (Sorg and Rohner 1996). Reproduction of the species is seasonal, with a 4-week mating season in May–June and a birth season in September–October (Ostner and Kappeler 1999; Barthold et al. 2009).

2. Data Collection

Between May to July and September to November, data were collected by doing focal scent-marking observations. Scent-marking behaviors were observed ad libitum during 27 to 34 half-days in each group. During these sessions, a total of 120 scent-marking behaviors (26 to 34 per group) served as foci for 15 minutes observations. During these 15 minutes observation periods we annotated for each individual passing on the focal spot, its identity, whether it performed anogenital scent-marking, or not, the date, the time, the context, and the identity of all the other individuals present in the 3, 5 and 10 meters ranges.

3. Data analyses

a. Audience characterization

For each passage with and without scent-marking, I characterized the audience composition by calculating the proportions of adult males and adult females present in the 0 to 3, 0 to 5, and 0 to 10 meters ranges of the focal individual.

b. Estimation of the audience effect on anogenital scent-marking

For a given individual, I only considered anogenital scent-marking events that occurred with a time-lapse of at least 5 minutes between each other. I selected passing events on the same criteria. I excluded 3 males from the dataset to only consider individuals from which I had at least 2 observations of each behavior (pass or mark). The three males excluded from the analyses were the three males that emigrated during the study period. The final male dataset included 14 individuals (4 sub-adults and 10 adults) observed for 60 pass and 105 anogenital scent-marking events. The female dataset included 11 adult females observed for 44 pass and 118 anogenital scent-marking events.

To model, for both sexes, the influence of the audience composition on the probability of anogenital-marking behavior to occur I run two independent Generalized Linear Mixed

Models (GLMM) with a binomial error structure and logit link function (Baayen et al. 2008) for each audience range. These models were fitted with R (version 3.6.0; R Core Team 2019) and RStudio (version 1.2-1335; RStudio Team 2018) using the function glmer of the R package lme4 (version 1.1-21; Bates et al. 2015) with the optimizer 'bobyqa". As fixed effects, I included in the model the proportions of males and adult females present in the given distance range. To control for age (for males only as there was only one age class for females), context and season I also included these terms in the model as control predictors. Individual identity and date were included as random factors to account for individual variations and the possible effect of particular events.

To reduce the risk of type I errors (Forstmeier and Schielzeth 2011), I included all possible random slope components (the proportion of males, the proportion of adult females, context, and season within individual identity). I manually dummy coded and then centered context, season, and age and z-transformed the proportion of males and the proportion of females before including them as random slopes. Initially, I also included all correlations among random intercepts and slopes for both models. However, for females, these were all estimated to have absolute values being essentially one indicating that they were not identifiable (Matuschek et al. 2017). Hence, I removed these correlations from the female model.

As an overall test of the effect of audience composition on the probability to anogenital scent-mark, I compared the full model with the null model lacking the fixed effects characterizing the audience (proportion of males and proportion of females) but comprising the control fixed effects and the same random effect structure as the full model (Forstmeier and Schielzeth 2011). This comparison was performed using a likelihood ratio test (Dobson 2009).

Model stability was assessed by comparing the estimates of the model run on the full dataset with the ones run on datasets, excluding each level of the random effects one after the other (Nieuwenhuis 2012). The models were relatively stable (for males: Supplementary Figure III.1.a; for females: Supplementary Figure III.2.a). To control for potential collinearity problems, I calculated the Variance Inflation Factors (Field 2005) for the model excluding the random effects. VIF values ranged from 1.05 to 1.37 for the males (Supplementary Table III.1.b) and from 1.08 to 2.13 for females (Supplementary Table III.2.b).

Confidence intervals were derived using the function bootMer of the package lme4, using 1,000 parametric bootstraps and bootstrapping over the random effects too (argument 'use.u' set to TRUE). Tests of the individual fixed effects were derived using likelihood ratio tests (Barr et al. 2013; R function drop1 with argument 'test' set to "Chisq"). I determined the proportion of the total variance explained by the fixed effects (R^2_m; marginal coefficient of determination), and the proportion of the variance explained by both fixed and random effects (R^2_c; conditional coefficient of determination) following the method recommended by Nakagawa et al. (2017) and using the function r.squaredGLMM of the package MuMIn (version 1.43.6; Barton 2019).

Because the models seem to suffer singularity issues, I further applied a Bayesian method as recommended by the authors of the "lme4" package (Bates et al. 2015). This approach should allow both regularizing the model via informative priors and giving estimates and credible intervals for all parameters that average over the uncertainty in the random-effects parameters. I fitted hierarchical linear models with the same structure as the ones described above using the R package "bmrs" (Bürkner 2018) based on Stan modeling language (Carpenter et al. 2017). I used the default priors, namely a Student's t-distribution ($\nu=3$, $\mu=0$, $\sigma=10$) for standard deviation for the likelihood function and unbiased priors for regression coefficients. Ten sampling chains were run for 6000 iterations and a warm-up period of 2000 iterations each. As the different traces overlap (Supplementary Figure III.1.c & Supplementary Figure III.2.c.) and that all $\hat{R}$-values were equal to 1.00 I considered that the chains sufficiently converged. Additionally, to check whether these models reflect the observed data, I compared the samples from the posterior predictive distribution to the observed data using the function "pp_check()". I reported for each variable the expected values under the posterior distribution and its 95% credible intervals (CIs). I judged that I had compelling evidence of an effect when 0 was not included in the 95% CI.

III. Results

In males the audience composition within a 3m distance range influenced the probability of anogenital scent-marking (full-null model comparison: $\chi^2=6.37$, df=2, P=0.041; $R^2_m=0.07$, $R^2_c=0.29$; inter-individual variation: s.d.=0.29). Particularly, males anogenital marked less when an increased proportion of males were present within the 3m range ($\chi^2=6.20$, df=1, P=0.013, Table III.1, Figure III.1.a.). There was also a tendency for males to anogenital mark more often when more females were present within the 3m range ($\chi^2=4.14$, df=1, P=0.042, Table III.1, Figure III.2.a.). However, the audience composition within the 5 and 10 m ranges did not influence the probability of anogenital scent-marking in males anymore (full-null model comparisons: for 5 m, χ^2=4.77, df=2, P=0.092, Table III.2; Figure III.1.b. & Figure III.2.b; for 10 m, χ^2=1.47, df=2, P=0.481, Table III.3, Figure III.1.c. & Figure III.2.c). For all three distance ranges, neither age, context, nor season had a significant effect on the probability of anogenital scent-marking in males (Table III.1, Table III.2 & Table III.3).

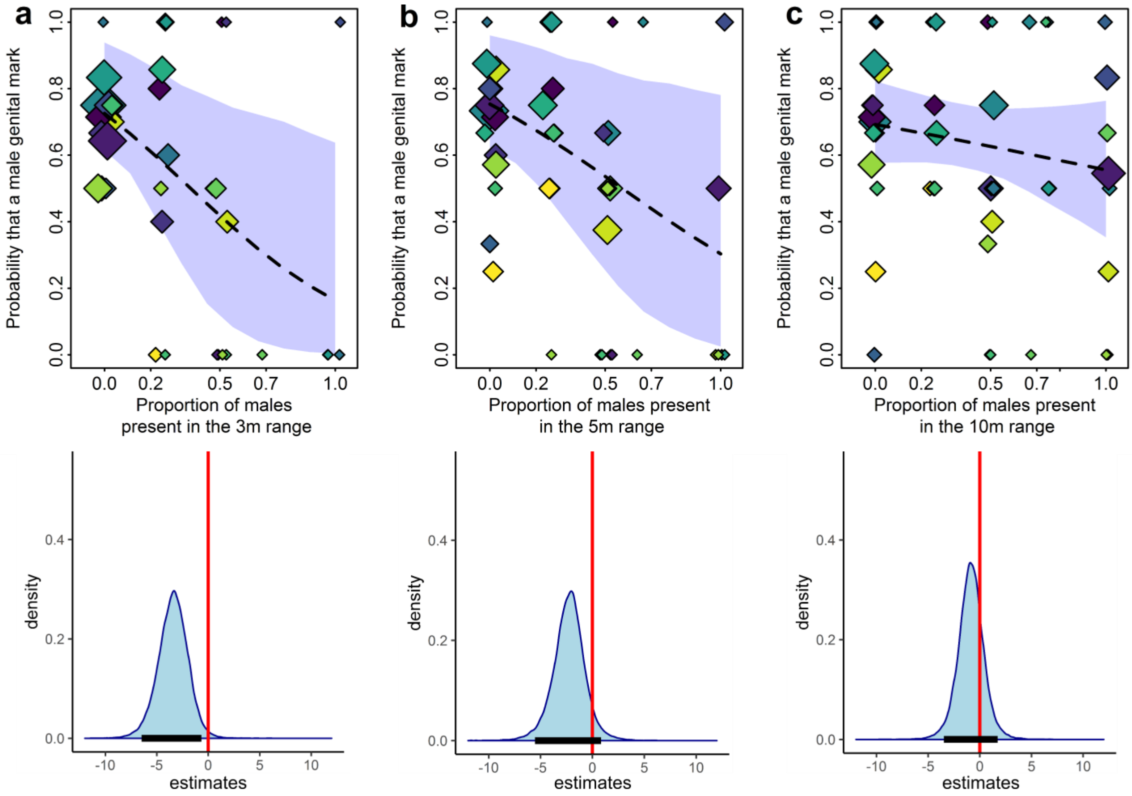


Figure III.1: Probability that a male genital-mark depending on the proportion of males present in a)3m, b)5m, c)10m. Colors correspond to the different individuals (n=14) and the size of the circle corresponds to the number of observations (n=165). Below each graph, I present the corresponding expected values under the posterior distribution and its 95% credible intervals (CIs) obtained with the Bayesian approach.

Table III.1: Results of the model of the effects of audience composition with 3m range, age, context and season on the probability that a male anogenital mark when passing a scent-marking spot.

	Frequentist approach									Bayesian approach			
	estimate	**standard errors**	**lower CI**	**upper CI**	**chi-squared**	**df**	**p-value**	**minimum**	**maximum**	**estimate**	**estimation error**	**lower CI**	**upper CI**
Intercept	0.26	0.46	-0.97	1.65	-	-	-	-0.17	0.48	0.37	0.67	-0.96	1.72
Proportion of males in 3m*	-2.60	0.98	-7.63	-0.61	6.20	1	**0.013**	-3.67	-2.12	-3.44	1.47	**-6.48**	**-0.67**
Proportion of females in 3m*	1.30	0.96	-0.67	4.85	4.14	1	**0.042**	0.95	2.79	1.74	1.4	-0.78	4.78
Age - Sub-adult	0.45	0.53	-0.64	2.01	0.91	1	0.341	0.11	0.76	0.17	0.66	-1.11	1.49
Context - Intergroup encounter	0.58	0.65	-0.87	3.45	1.02	3	0.795	0.35	1.36	1.26	1.01	-0.45	3.57
Context - Resting	0.17	1.28	-5.68	8.77				-0.37	1.45	0.45	1.8	-3.00	4.36
Context - Traveling	0.13	0.54	-1.24	1.75				-0.03	0.73	0.4	0.73	-0.99	1.89
Season - Mating	0.43	0.77	-1.37	5.26	0.43	1	0.511	0.12	0.74	0.36	1.19	-2.01	2.77

Table III.2: Results of the model of the effects of audience composition with 5m range, age, context and season on the probability that a male anogenital mark when passing a scent-marking spot.

	Frequentist approach									Bayesian approach			
	estimate	standard errors	lower CI	upper CI	chi-squared	df	p-value	minimum	maximum	estimate	estimation error	lower CI	upper CI
Intercept	0.67	0.55	-0.64	2.68	-	-	-	0.38	0.89	1.08	0.88	-0.58	2.92
Proportion of males in 5m	-1.95	0.86	-5.71	-0.11	6.89	1	**0.009**	-2.46	-1.08	-2.26	1.58	-5.54	0.84
Proportion of females in 5m	0.36	0.79	-1.94	2.92	0.21	1	0.643	0.05	0.88	0.33	1.21	-1.98	2.84
Age - Sub-adult	0.69	0.55	-0.45	2.61	1.68	1	0.195	-0.01	0.89	0.29	0.76	-1.13	1.88
Context - Intergroup encounter	0.49	0.60	-1.07	3.56	1.29	3	0.731	0.30	0.97	1.4	1.11	-0.43	3.93
Context - Resting	0.15	1.80	-8.41	10.07				-0.49	4.78	0.09	2.1	-3.97	4.75
Context - Traveling	-0.18	0.59	-2.34	1.37				-0.46	0.17	-0.01	0.86	-1.67	1.72
Season - Mating	0.37	0.84	-1.77	5.22	0.19	1	0.664	-0.03	0.71	0.02	1.45	-2.87	3.03

Table III.3: Results of the model of the effects of audience composition with 10m range, age, context and season on the probability that a male anogenital mark when passing a scent-marking spot.

	Frequentist approach									Bayesian approach			
	estimate	**standard errors**	**lower CI**	**upper CI**	**chi-squared**	**df**	**p-value**	**minimum**	**maximum**	**estimate**	**estimation error**	**lower CI**	**upper CI**
Intercept	0.70	0.60	-0.31	1.86	-	-	-	0.38	0.96	1.46	1.11	-0.49	3.95
Proportion of males in 10m	-0.97	0.70	-1.91	0.59	1.13	1	0.287	-1.32	-0.44	-0.87	1.29	-3.49	1.72
Proportion of females in 10m	-0.14	0.87	-1.33	1.27	0.01	1	0.942	-0.59	0.31	-0.54	1.26	-3.18	1.85
Age - Sub-adult	0.99	0.59	-0.87	0.95	0.01	1	0.904	0.22	1.57	0.29	0.89	-1.36	2.21
Context - Intergroup encounter	0.53	0.58	-0.17	2.25	2.29	3	0.515	0.26	1.00	1.54	1.16	-0.37	4.19
Context - Resting	0.58	2.11	-1.31	2.14				-0.56	14.90	0.15	2.41	-4.4	5.53
Context - Traveling	-0.23	0.60	-0.88	1.07				-0.46	0.10	-0.21	0.92	-2.13	1.53
Season - Mating	0.00	0.83	-1.35	1.30	0.01	1	0.924	-0.36	0.61	-0.21	1.72	-3.75	3.31

In females, the audience composition did not influence the probability of anogenital scent-marking (full-null model comparison: for 3m, χ^2=4.84, df=2, P=0.089, Table III.4; for 5 m, χ^2=6.85, df=2, P=0.032, Table III.5; for 10m χ^2=3.54, df=2, P=0.171, Table III.6). Neither the proportion of males, the proportion of females, age, context, nor season predicted anogenital scent-marking rates (Table III.4, Table III.5 & Table III.6).

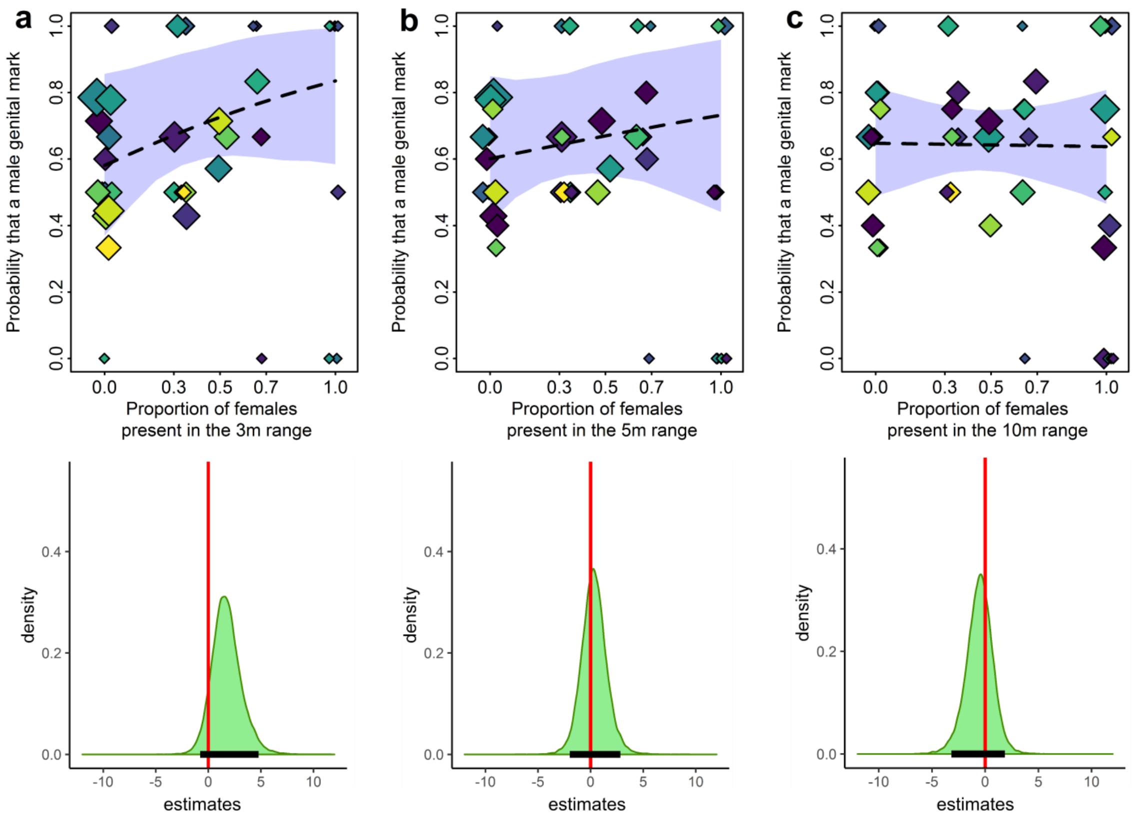


Figure III.2: Probability that a male genital-mark depending on the proportion of females present in a)3m, b)5m, c)10m. Colors correspond to the different individuals (n=14) and the size of the circle corresponds to the number of observations (n=165). Below each graph, I present the corresponding expected values under the posterior distribution and its 95% credible intervals (CIs) obtained with the Bayesian approach.

Table III.4: Results of the model of the effects of audience composition with 3m range, context and season on the probability that a female anogenital mark when passing a scent-marking spot.

	Frequentist approach									**Bayesian approach**			
	estimate	**standard errors**	**lower CI**	**upper CI**	**chi-squared**	**df**	**p-value**	**minimum**	**maximum**	**estimate**	**estimation error**	**lower CI**	**upper CI**
Intercept	1.41	0.39	0.71	2.44	-	-	-	-0.17	0.48	1.71	0.59	0.63	2.96
Proportion of males in 3m	-0.67	0.84	-2.62	1.34	0.64	1	0.425	-3.67	-2.12	-1.1	1.27	-3.71	1.32
Proportion of females in 3m	-0.71	0.71	-2.50	0.78	1.00	1	0.319	0.95	2.79	-0.47	1	-2.41	1.54
Context - Intergroup encounter	-0.10	0.53	-1.20	1.23	1.01	3	0.799	0.11	0.76	0.03	0.91	-1.59	2.00
Context - Resting	0.34	0.64	-0.92	2.75				0.35	1.36	0.45	1.06	-1.57	2.66
Context - Traveling	-0.30	0.49	-1.44	0.80				-0.37	1.45	-0.41	0.69	-1.78	0.94
Season - Mating	-0.13	0.48	-1.18	1.29	0.07	1	0.790	-0.03	0.73	-0.01	0.86	-1.54	1.87

Table III.5: Results of the model of the effects of audience composition with 5m range, context and season on the probability that a female anogenital mark when passing a scent-marking spot.

	Frequentist approach									**Bayesian approach**			
	estimate	**standard errors**	**lower CI**	**upper CI**	**chi-squared**	**df**	**p-value**	**minimum**	**maximum**	**estimate**	**estimation error**	**lower CI**	**upper CI**
Intercept	1.61	0.45	0.89	2.99	-	-	-	1.46	2.00	1.92	0.64	0.73	3.27
Proportion of males in 5m	-0.50	0.85	-2.49	1.35	0.34	1	0.558	-1.05	-0.07	-0.76	1.22	-3.16	1.66
Proportion of females in 5m	-0.95	0.66	-2.60	0.48	2.13	1	0.145	-1.29	-0.55	-0.83	0.92	-2.63	0.99
Context - Intergroup encounter	-0.09	0.53	-1.24	1.27	1.30	3	0.730	-0.44	0.17	-0.07	0.87	-1.71	1.75
Context - Resting	0.18	0.65	-1.30	2.53				-0.14	0.92	0.33	1.07	-1.65	2.53
Context - Traveling	-0.47	0.51	-1.79	0.64				-0.81	-0.26	-0.59	0.7	-1.99	0.77
Season - Mating	-0.02	0.49	-1.08	1.35	0.00	1	0.962	-0.29	0.22	0.1	0.83	-1.39	1.9

Table III.6: Results of the model of the effects of audience composition with 10m range, context and season on the probability that a female anogenital mark when passing a scent-marking spot.

	Frequentist approach									Bayesian approach			
	estimate	standard errors	lower CI	upper CI	chi-squared	df	p-value	minimum	maximum	estimate	estimation error	lower CI	upper CI
Intercept	1.95	0.68	0.99	5.00	-	-	-	1.68	2.40	2.07	0.76	0.68	3.66
Proportion of males in 10m	-1.75	1.00	-5.45	-0.06	3.01	1	0.083	-2.67	-1.34	-1.72	1.17	-4.11	0.54
Proportion of females in 10m	0.23	0.73	-1.48	2.45	0.11	1	0.745	0.03	0.96	0.3	0.82	-1.26	1.99
Context - Intergroup encounter	-0.07	0.56	-1.73	2.05	1.71	3	0.634	-0.35	0.30	-0.07	0.92	-1.75	1.87
Context - Resting	0.55	0.79	-1.11	6.57				0.21	1.44	0.76	1.14	-1.38	3.08
Context - Traveling	-0.55	0.61	-2.65	0.91				-0.92	-0.29	-0.55	0.75	-2.03	0.92
Season - Mating	-0.14	0.59	-1.69	2.21	0.06	1	0.813	-0.38	0.16	0.07	0.94	-1.65	2.14

IV. Discussion

In this study, I investigated intragroup audience effects on anogenital scent-marking behaviors in a wild population of red-fronted lemurs. I particularly investigated whether males and females differed in this aspect and if these differences may reveal functional differences associated with anogenital scent-marking across sexes. Here I discuss my results and the derived potential functional significance of anogenital scent-marking in red-fronted lemurs.

I found an intragroup audience effect in males but not in females. I predicted that females would anogenital scent-mark more in the presence of an increased proportion of females if they use anogenital scent-marking to synchronize their estrus. Considering the short fertile period of females, this female-female audience effect may still take place at a smaller time scale. Other passive or active mechanisms may also be responsible for this estrus synchrony.

For their part, male red-fronted lemurs were observed to anogenital mark significantly less often when an increasing proportion of males of their group were in their three meters range. I predicted the presence of an intragroup intra-sex audience effect particularly pronounced in males compared to females, due to their competition level. Indeed, males have been suggested to use anogenital scent-marking for advertising their social/reproductive status to other males of their group as a form of indirect competition. However, this male-male audience effect was not significant anymore when looking at the five- or ten-meters ranges.

Two main non-exclusive hypotheses may be suggested to explain the observed results of a male-male audience effect at the three meters range only. First, males may prefer to reduce the risk of physical aggression by avoiding to scent-mark near other males. Even if aggression rates are low, the risk of physical aggression may be increased in close proximity with males being less motivated or successful to physically reprimand another male scent-marking in the five- or ten-meters ranges. This hypothesis could be further tested by looking at the probability of aggression at different distances. Second, some males may give priority to other males to scent-mark the spot when they are in proximity. Hence, the competition between males may take place to have priority access to these specific scent-marking spots. At five or ten meters, the focal male may have sufficient time to mark before the arrival of a male for which at proximity he would give priority. If for instance, priority is given to the central males, it would also explain why central males are observed to scent-mark more frequently than subordinate males (Ostner and Kappeler 1999). A parallel can be drawn with the reproductive "priority of access model" supported in this species by the fact that the number of females in the group better predicted the subordinate probability to sire offspring than the number of males in the group (Kappeler and Port 2008). Central males are suggested to have priority to access a female over any other male; however, when an increased number of females are present, this priority becomes less constraining for subordinate males as the central male cannot simultaneously access several females.

Integrating the social status of the individuals (e.g., central or subordinate males) in the model would allow exploring these two non-exclusive hypotheses further. If this inclusion was not possible in the present study, my results still provide some information on this concern. First, I chose to characterize the audience using the proportion of individuals instead of the absolute number of individuals. This choice allows my results to be more informative about the effect of the composition of the audience. Indeed, if the presence of one or several specific individuals (e.g., central male) is targeted or avoided by a potential marking individual, then when the proportion of individuals of the given sex in the audience is 1, the targeted individuals are necessarily in the audience independently of the group size. Moreover, considering that the model individual variation was relatively high (s.d.=0.29; R_c-R_m=0.27), the observed audience effect may indeed be dependent on the status of a particular male.

Males also tended as predicted to anogenital mark more often when a higher proportion of females were in the three meters range, which suggests that these signals may also be addressed to females. However, this effect appeared to be quite moderate, so the decreased scent-marking effect due to the presence of males seems to prevail over it. Hence, when given the possibility to mark by the male audience, males may be encouraged to mark in the presence of females in the three-meters range. Puzzlingly, this effect was also not significant at the five- and ten-meters ranges.

The loss of audience effects observed at larger distances could also be suggested to be the result of an altered picture of the audience with increasing distances. These animals indeed live in a forest environment where visibility rapidly decreases with distance. However, as we were able to assess the audience composition until ten meters reliably and that they probably additionally rely on their olfactory and auditory senses to assess their audience composition, decreased visibility is unlikely to have impacted their knowledge on audience composition. Another possibility to explain the absence of audience effects observed at larger distances may be because the probability for an individual that already passed the scent-marking spot location or surroundings to return to this spot location seems relatively low (personal observations). Considering the directionality of the individuals in the audience may also be an interesting perspective in this regard. While at three meters, the individuals may be relatively homogeneously attentive to the scent-marking of an individual, at five and ten meters, the directionality of the individuals in the audience may be more important to consider. Individuals approaching the scent-marking spot may indeed be more attentive than the individuals that already overpassed this spot.

Besides these intragroup functions, scent-marking may also be a form of intergroup communication, with a function of resource or territorial defense through individual or group odor deposition (Pereira et al. 1988; Stockley et al. 2013; Tinsman et al. 2017; Janda et al. 2019). Female red-fronted lemurs are philopatric and inherit the territory of their mother, so they may have an especially steep interest in defending their territory and/or its associated resources. They have indeed been shown to take part in intergroup interactions more often and more aggressively than males (Pyritz 2011). Here I explored only intragroup audience effects, but exploring intergroup audience effects would bring interesting information to complete the full picture of anogenital scent-marking functions in red-fronted lemurs.

Audience effects are usually tested by comparing control scan conditions when the targeted behavior is not expressed with conditions when the targeted behaviors are expressed (e.g., in Baniel et al. 2019). In this study, I estimated that the effect of motivational state might be too important, and this traditional approach may have been irrelevant. To reduce this potential effect of motivational state, I decided to consider instead of control scans, occurrences of passing without exhibiting scent-marking on a scent-marking spot. Marking spots were defined as such if any individual of the focal group scent-mark the exact spot location in a 15 minutes window period. In this way, I hope to reduce the effect of different motivational states, as at least one individual of the group expressed his motivation to scent-mark this specific location at that time.

If this protocol appeared adequate, it still presents some limitations concerning the control of the individual's motivational state. First, I cannot exclude and control for the existence of an audience effect on the probability to pass or not on this specific spot. Some individuals may also in the presence of a particular audience choose not even to pass on this specific location. Second, the effect of who may have marked beforehand on a specific spot may also be highly relevant in the choice of an individual to mark or not when passing on a spot. This parameter is hard to control, first because I do not have information on the possible passage on this spot before the start of the video recording (and olfactory signals are long-lasting) and second because multiple individuals may have marked the same spot before the arrival of a focal individual. Considering this parameter would drastically increase the complexity of the models and would require a significant increase in sample size. Further studies on the patterns of scent-marking behavior succession occurring on a given scent-marking spot may help to uncover these questions. These limitations may contribute to explain why the observed audience effects were relatively small. Nevertheless, if they were small, I believe that the use of combined statistical methods assures the robustness of the effects presented in this study.

By the present work, I first contribute to the study of both scent-marking and audience effects that have rarely been addressed in the wild. Second, I provide important insights into the functional significance of anogenital scent-marking in red-fronted lemurs and its associated sex differences. In true lemurs, genital and perianal secretions were shown to be chemically more complex in egalitarian species living in multi-males-multi-females groups than in species living in pairs and/or having female dominance (delBarco-Trillo et al. 2012). This increase in complexity was shown to be particularly significant in males (delBarco-Trillo et al. 2012; delBarco-Trillo and Drea 2014). The results of this study are concordant with the idea of a greater level of intragroup social pressures associated with anogenital scent-marking in males than in females in these species.

Moreover, by studying the flexibility of usage of complex signals, as scent-marking behaviors, across social contexts (audience compositions), this work also contributes to uncovering potential social selective pressures that may have led to the evolution of flexible signals (Peckre et al. 2019). Here I considered a fixed multimodal signal, the visual display, and the scent deposition being inseparable. Some structural modifications may happen by modifying the intensity of the visual display; however, this is hard to quantify objectively, so here I focused on signal occurrence. In our observations, anogenital scent-marking seemed to be increased in males in the absence of other males which goes against the demonstrative marking hypothesis. Hence the social pressures at play between males do not seem to be at the origin of the multimodal nature of these signals but may have rather constituted pressures to adopt certain behavioral flexibility.

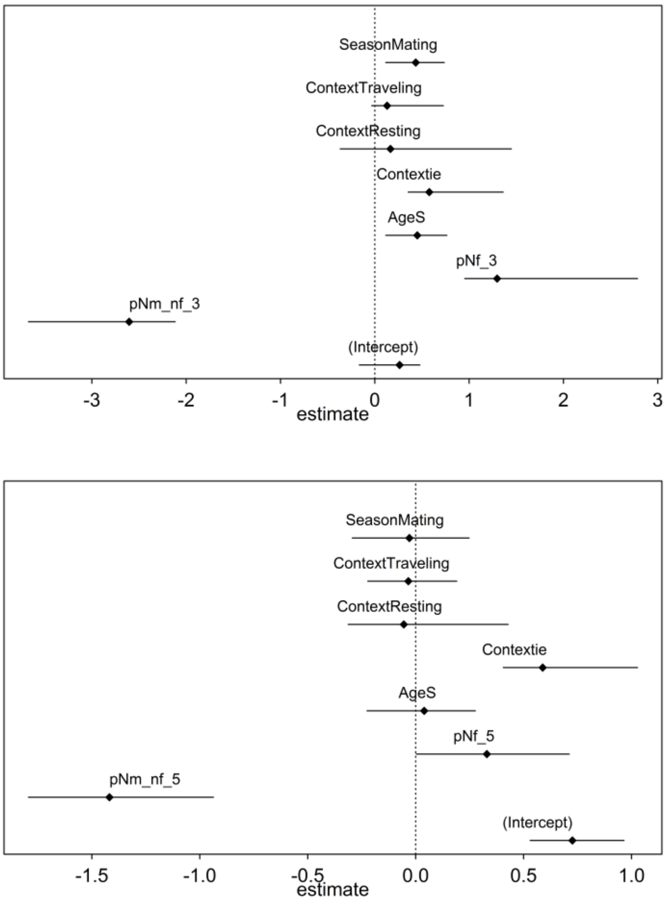
V. Acknowledgements

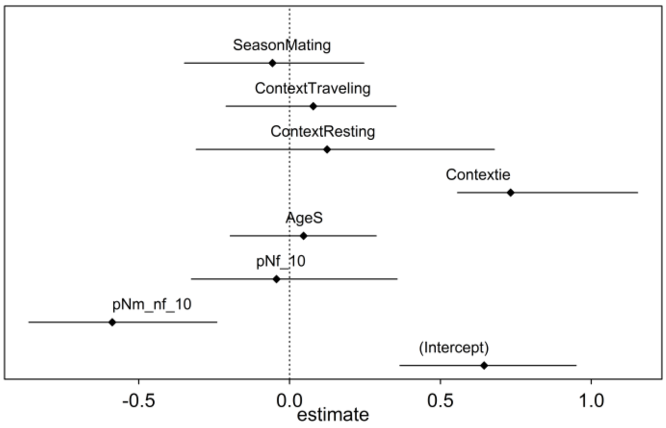
I warmly acknowledge Franziska Hübner for her relevant comments on the data analyses. I am most grateful to the local team of the Kirindy field station. I thank the Malagasy Ministère de l'Environnement et des Eaux et Forêts, the Département de Biologie Animale of Antananarivo University, and the Centre National de Formation, d'Etudes et de Recherche en Environnement et Foresterie for supporting and authorizing long-term research in Kirindy. This study was funded by the Deutsche Forschungsgemeinschaft (DFG FI 929/13-1) (DFG FI 929/21-1). Fieldwork was conducted by the German Primate Center in Kirindy with the authorization of the Commission Tripartite de la Direction des Eaux et Forêts. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

VI. Supplementary material

Appendix 1: Model for the males

Supplementary Figure III.1.a. Stability of the estimates for the males

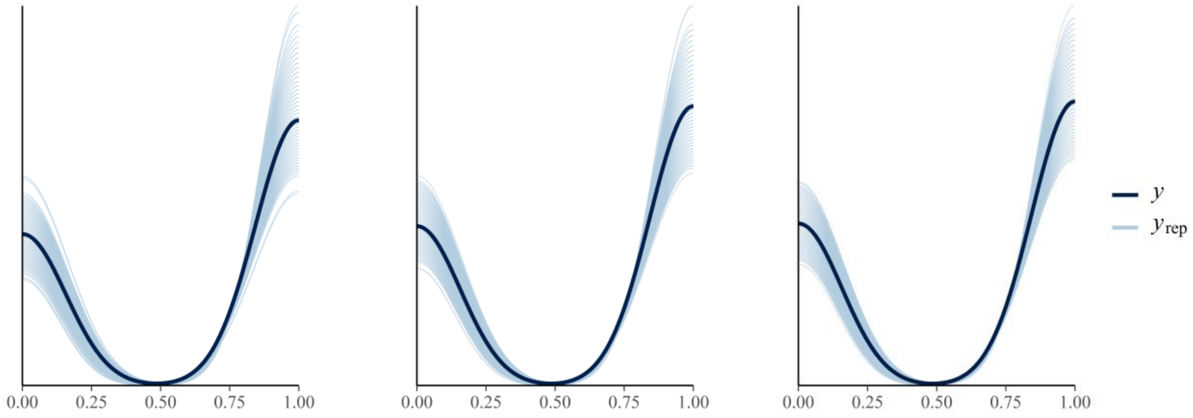




Supplementary Table III.1.b. Variation Inflation Factors for the male model

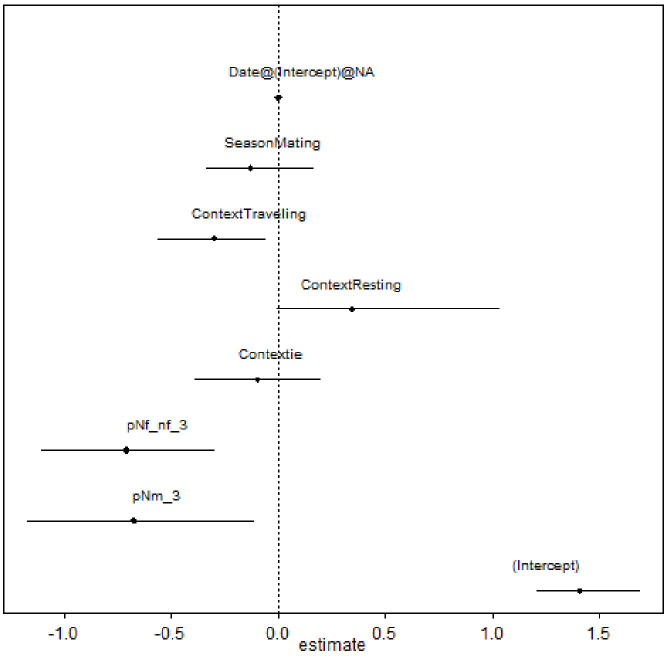
	3m	5m	10m
Proportion of females	1.35	1.54	1.77
Proportion of males	1.15	1.27	1.41
Age	1.05	1.04	1.06
Context	1.08	1.14	1.12
Season	1.13	1.09	1.04

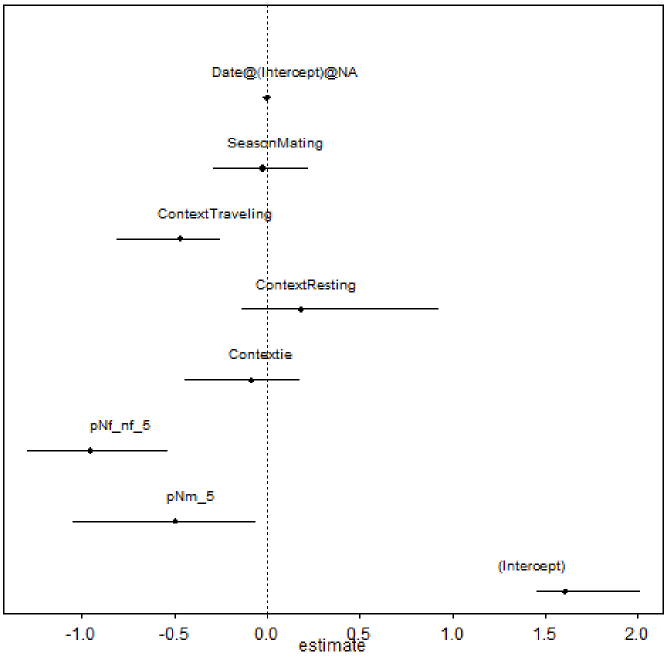
Supplementary Figure III.1.c. Traces overlap for the male models for 3m, 5m and 10m ranges

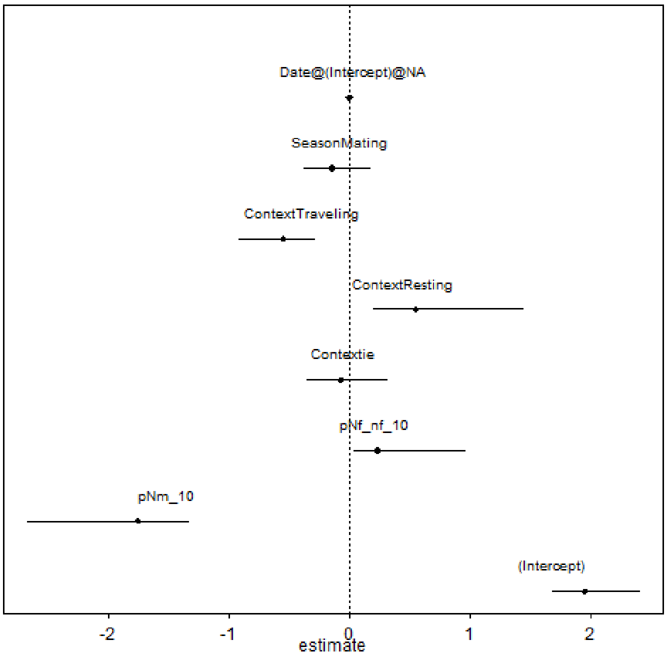


Appendix 2: Model for females

Supplementary Figure III.2.a. Stability of the estimates for the females



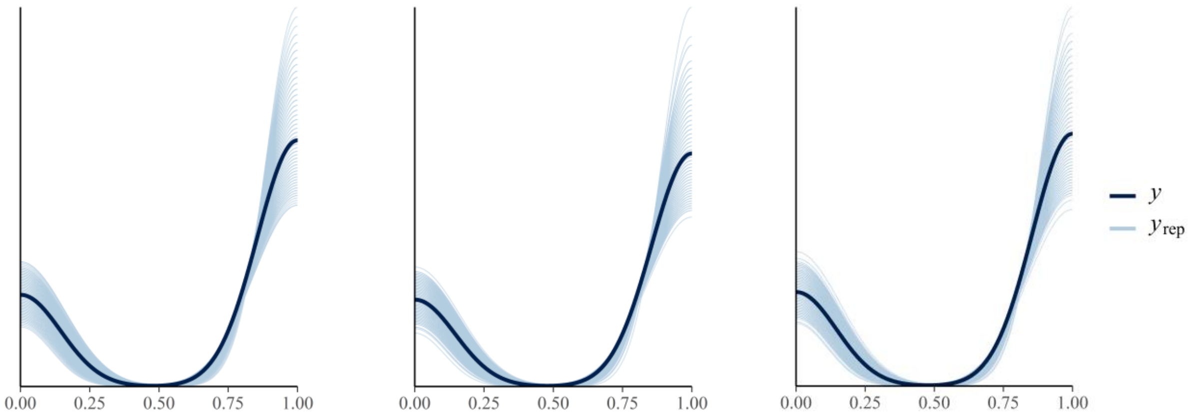




Supplementary Table III.2.b. Variation Inflation Factors for the female model

	3m	5m	10m
Proportion of females	2.12	2.20	1.80
Proportion of males	2.03	2.25	1.83
Context	1.07	1.09	1.11
Season	1.08	1.09	1.07

Supplementary Figure III.2.c. Traces overlap for the female models for 3m, 5m and 10m ranges



Chapter IV: On the look for mongoose lemurs or how I learned my first Malagasy sentence: “Tsy misy kakazo maventy”*

Personal report of the work and process that led to the study of *E. mongoz* in Ankatsabe forest. Not intended to be published elsewhere.

** There are no more big trees*

I. Rationale

If large-scale studies including many different species are of great interest, I argue that small-scale comparisons associated with a more holistic description of the complexity of the given systems may also be a highly informative complementary approach. Even though lemurs are conspicuously vocal, also rely heavily on olfactory communication, and have a well-developed visual sense, their communicative system remains poorly studied. Since they also have complex social structures despite their primitive physical characteristics and relatively small brains (Oda 2008), they provide an excellent model to test the social complexity hypothesis.

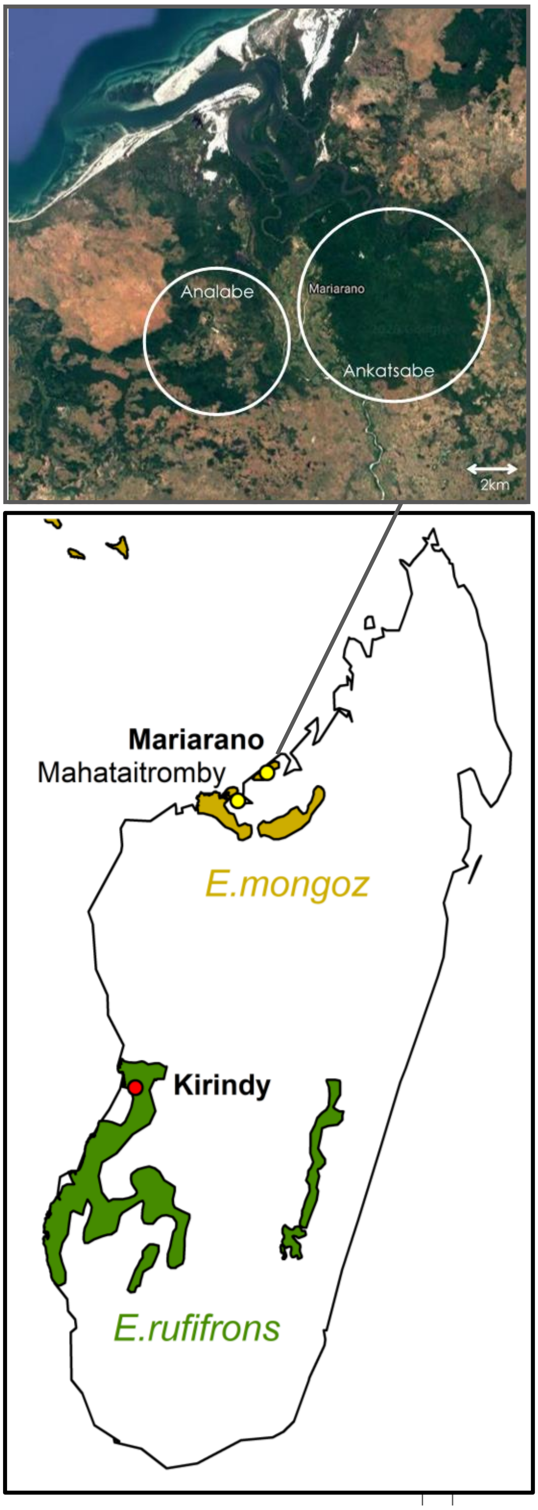


Figure IV.1: Distribution areas of *E. rufifrons* and *E. mongoz* (IUCN, 2012) and locations of the different field site visited. The zoomed map is from Images © 2020 CNES / Airbus, Maxar Technologies, données cartographiques © 2020 adapted based on Ibouroi et al. 2013.

We argued earlier that any comparative study on communication should include considerations about habitat and morphological differences between species as well as their phylogenetic relationship (Ramsier et al. 2012; Manser et al. 2014; Peckre et al. 2019). Among lemurs, the “true lemur genus” (Eulemur) contains twelve different species all endemic to Madagascar (Markolf and Kappeler 2013). These medium-sized primates, offer an excellent opportunity to study closely related species, having comparable morphology, living in a comparable habitat but differing in their social system. Indeed, they live in different group sizes (Ossi and Kamilar 2006; Kappeler and Fichtel 2015) and if female dominance characterizes most of the Lemuridae species, the Eulemur clade contains few exceptional species in which both sexes are codominant.

Among these codominant species, I could study a habituated population of *E. rufifrons*, a species described as promiscuous and egalitarian living in multimale-multi female groups in the dry deciduous forest of Kirindy (Figure IV.1). Besides, true lemurs are also of particular interest because they constitute the only case of potential transition from a group living ancestor to social monogamy (Lukas and Clutton-Brock 2013; Kappeler 2014) offering a unique opportunity to test the effect of the selective pressures associated with social monogamy. Only two true lemur species, the red-bellied lemurs (*E. rubriventer*) and the mongoose lemurs (*E. mongoz*) have been described as socially monogamous. My choice was straightforwardly directed to the *E. mongoz*. Indeed, while *E. rubriventer* is living in the tropical rain forest, *E. mongoz* inhabit dry deciduous forests comparable to the ones hosting *E. rufifrons* (Figure IV.1).

II. Looking for a possible field site to study mongoose lemurs

To my knowledge, there has been no long-term research carried out on mongoose lemurs in the wild. Moreover, since 2012, this species is considered to be critically endangered (IUCN 2012) with an estimated loss of 80% of its population over 20 years due to habitat loss and hybridization with *E. rufus* (Pastorini et al. 2009; IUCN 2012). Therefore, one of the first steps of my project was to find an appropriate population of *E. mongoz* to study.

I first started the search for it by reviewing the literature of research carried out on wild populations of *Eulemur mongoz* in Madagascar. I could only find a handful of papers and most of them were published 15 to 20 years ago. I contacted the studies' authors, but the few testimonies gathered were in the image of the one of Jennifer Pastorini: “I did my fieldwork in 1997, that is nearly 20 years ago! As far as I know, the forest where I worked and which was full of lemurs at that time, has now entirely been cut” (January 23rd, 2016). Only one paper was published more recently by Nadhurou et al. (2015). He recorded *E. mongoz* individuals in three different sites in Madagascar. In this paper, he described Bombetoka-Belemboka, the field site where he could record the most individuals (25/42), as “a New Protected Area (NAP)” that “covers a total area of 71.943 ha of mangroves and dry deciduous forest”. Hence, this appeared as a good field site candidate. This possibility was also later confirmed to me by Dr. Rodin Rasoloarison, professor at the University of Antananarivo and administrative assistant in Madagascar for my department and Pr. Solofonirina Rasoloharijaona, professor at the University of Mahajanga.

1. Bombetoka-Belemboka expedition (2016 May 22nd to 26th)

Following the pilot study, I carried out on *E. rufifrons* at Kirindy forest (Figure IV.1) from March to May 2016, Rodin Rasoloarison and I went for a short field recognition expedition in the Bombetoka-Belemboka area (May 22nd to 26th). We were welcomed and allowed to establish a camp in the village of Mahataitromby (Figure IV.1) accessible by boat from Mahajanga and where Bakri Nadhurou based his research in July and August 2008. At that time, he could record 7 groups of *E. mongoz* ranging from 3 to 6 individuals (Nadhurou et al. 2015) in three different sites: Amboaniokely, Antsakanalabe, and Andohan'ny sankoanybe.

a. Visit of the potential study sites

On the afternoon of May 23rd (15h-18h), we visited the first site called Amboaniokely consisting of a rocky islet of a few kilometers length located 30 minutes from the camp. During the wet season, this islet is surrounded by the sea but from April it is also accessible by feet. In September-October 2015, 3 groups of *E. mongoz* had been identified in this area. The difficult accessibility, the fact that the land is sloped, and a local honey-production apparently protect this site from deforestation. However, despite dense vegetation in most of the parts we visited, we found an area, known to be the territory of one group, recently destroyed by a fire. We did not find any *Eulemur mongoz* group that day.

Figure IV.2: Antsakanalabe site

The next days (May 24th 7h-13h & May 25th 9h-14h) we went to Antsakanalabe a site consisting of a long narrow strip of trees on the border sides of a dry river bed which extends between 45 to 90 minutes from camp (Figure IV.2). On the first kilometer, an old transect also existed on one side. The vegetation was quite dense but the forest strips were most of the time not larger than 50 meters. Several groups had been regularly identified in this area between 2006 and 2011. We discovered that this site was suffering from active deforestation, most of the big trees having been cut and fresh cart trails and coal production installations being visible around this site (Figure IV.3) to the astonishment of our guides.

Figure IV.3: Active deforestation in Antsakanalabe

On the 24th of May, we found 1 group of 6 individuals (3 males, 2 females, 1 juvenile male), that we observed for 1-2 hours (Figure IV.4). The vegetation was dense rendering our movements difficult but we had good visibility of the animals. The group split when our guide yelled to call us but when we found them back, they did not flee away or neither vocalized although they kept staring at us until we left. On the 25th of May, our guide found another group, but we quickly lost track of them.

Figure IV.4: *Eulemur mongoz* (a. female; b. male) in Antsakanalabe

In 2015, 3 groups were also identified in the site of Andohan'ny sankoanybe, but since then this site had been so degraded that my guide considered that it was not even worth visiting it.

b. General information gathered on-site

We could gather additional information among the villagers and learned that between 2005 and 2011, this area had been the place of several conservation and development projects first within the framework of the Voronosy Project implemented by Mario Perschke, and then, by the association Fanamby which took over these activities after his death in 2007. Most probably for political reasons (unclear to us), Fanamby stopped its activities in this site after 2011. Since then, deforestation and hunting activities have escalated. Besides, my guides also reported common group sizes greater than expected for this species (up to 8 individuals) in the area. I assumed that this was probably the result of the pressures associated with the loss of habitat and forest fragmentation making migrations impossible.

c. Time to take stock

From a logistic point of view, the installation in this site wouldn't lead to significant problems and our presence seemed to be well accepted by the local population. An important population of habituated *Eulemur mongoz* was still present a few years before our visit and there were probably still several groups around at the time of our visit. However, We discovered that this area became highly fragmented in the last years preceding our trip and still suffered at the time of our visit from active and intensive deforestation and hunting activities. Probably as a result of these, the local *E. mongoz* population previously known to be habituated seemed to become wilder and to modify their social behavior (increased group size).

Hence, I identified two major problems preventing us to work in this area. First, the re-habituation of the animals may have been difficult and more importantly, if managed successfully, it would have highly exposed these individuals to hunting. Second, given the intensive deforestation we could observe, it was even difficult to predict which proportion or whether some of the forest (and animals) would have been remaining the next year (when the field season was planned). Hence, it frustratingly and sadly appeared clear to me that it was better to renounce to pursue research on this site.

2. A new perspective for a field site: Ankatsabe forest

a. *A new track*

On the way back from Mahaitromby, we met in Mahajanga, Dr. Herimalala Raveloson who informed us of the presence of several groups of *Eulemur mongoz* in the Mariarano municipality (Figure IV.1). He stated that in this region, the lemurs are better protected because considered as sacred. However, I previously excluded this area of the possible study sites as Bakri Nadhurou reported that in the "Ankatsabe-Analabe forest […] located in the Mariarano municipality, […] mongoose lemurs are severely hunted for food" (Nadhurou et al. 2015). He studied in this area 2 groups of 2 and 5 individuals.

If during Bakri Nadhurou's study (2008 to 2010), the two forest fragments Ankastabe and Analabe seemed to be connected and present similar characteristics, some ensuing literature research revealed a new dichotomy between the Analabe and Ankatsabe fragments. In 2013, Ibouroi and colleagues reported for the Analabe fragment (Figure IV.1): "we noted several signs of deforestation […] and that the culture of land burning is abundant. We did not note any trace of hunting. Last year a bush fire swept the forest and overwhelmed its western part. As a result of this, only a small part of the forest cover remains". Contrastingly, they reported for the Ankatsabe fragment (Figure IV.1): "Our observations showed little signs of human deforestation for wood-work and wood fire chambers. We found no trace of hunting." These authors also reported 6 *E. mongoz* individuals observed for a 16.7 km survey effort in this forest fragment. Hence, I decided to pursue the research on the site of Ankatsabe forest.

b. *Activities in Ankatsabe forest*

Ankatsabe forest surrounds the village of Mariarano (Figure IV.1), it is an unprotected western dry deciduous forest block situated 50km northwest of Mahajanga. By not being protected, the area is clearly at risk of loss and reduction in the quality of habitat. If most of the plantations (rice, manioc, and maize) are intended for local consumption only, charcoal production destined for sale in Mahajanga is increasing and comes directly from the burnt forest (Long et al. 2012).

Nevertheless, the Ankatsabe forest fragment was considered to show a high degree of preservation compared to other non-protected areas with fewer fires detected and constant lemur relative abundances (Long et al. 2012). Some forest and mangroves restoration initiatives having even seen the light (Long et al. 2012; Deutsche Gesellschaft für Internationale Zusammenarbeit (Programme Germano-Malgache pour, l’Environnement PGM-E/GIZ 2014). Additionally, some „fady“ (forbidden by customs) seems to reduce hunting pressure on lemurs effectively.

Since 2009, a collaborative project involving the local community forest management group of Mariarano (VOI), Development and Biodiversity Conservation Action for Madagascar (DBCAM), a Malagasy conservation NGO, Operation Wallacea, an international volunteer-based NGO that supports conservation research through academic partnerships and the University of Antananarivo has been assessing the forest’s biodiversity. Ankatsabe forest seems to host at least 21 mammal species, 50 reptile species, 9 amphibian species, and over 70 bird species. Among mammal species, 9 are lemur species (*Cheirogaleus medius*, *Propithecus coquereli*, *Lepilemur edwardsi*, *Eulemur mongoz*, *Eulemur fulvus*, *Avahi occidentalis* and *Phaner pallescens*).

c. *The option is being confirmed*

Between June 2016 and March 2017, I established contact with several people working or having been working in Mariarano. These exchanges allowed me to consider this site as a viable option. My interlocutors indeed confirmed the presence, relatively sparse but constant, of the *E. mongoz* in the area and the relatively low hunting pressure due to the existence of “fady” (forbidden specified by the customs) and the fear of the VOI’s laws and repression.

I could also gather useful information concerning logistics. First, the local forest management committee (VOI) owned and managed a camping site at the entrance of the village. Every year, the collaborative project mentioned above takes the form of a 2-month field-course in June-July. The DBCAM team usually arrives on-site in April to prepare the camp before the students' arrival. Hence, two options appeared possible for me from a logistic point of view, either joining the DBCAM team or rent a small camping area and implement a new work team.

Joining the DBCAM team would have guaranteed for a fee the provisioning and energy supply and would have alleviated the employment of cook(s) and guide(s). However, the corresponding fees would have represented considerable costs for my project. Moreover, this option would have prevented us from some independence and flexibility concerning the guides' availabilities and meal times. Considering these constraints, and some warnings I received concerning disagreements and conflicts between the VOI and the DBCAM during the precedent years, I chose the second option. This second option consisted of renting a small part of the camping area to the VOI and built an independent team. This option reduced our global costs, allowed me more flexibility, more neutrality regarding potential conflicts, and provided more direct incomes for the local community. However, this solution was coupled with more logistics to manage for the provisioning, no electricity supply, and a direct employment relationship between me and the other members of the team.

Figure IV.5: Our camp in Mariarano village

III. Mariarano expedition (2017 May 10th-July 28th)

1. Arrival and logistics

Beginning of May 2017, I met in Antananarivo Basile Andriambeloson, master student at the University of Antananarivo. He was my assistant and translator for the whole field period. We left together for Mahajanga where we spent a few days making the permit certified by the DREEF and other local institutions and organizing the first provisioning. Once we arrived on site on May 13th, we directly met the Maire, the VOI director, and the DBCAM director. I was introduced to two cooks and two guides that I later employed after negotiating salaries following the requisitions of the VOI and aligned to the ones offered by the DBCAM. The final team was composed of Basile Andriambeloson, two guides Janoarisaona Randrihaniharisoa (Ihari) and Armand-Célestin Tsimanihitra, two cooks Lydia Raharisoa (Mino) and Mônique Rayanadramiasy, Lilas Allard, a French master student that joined us for the second half of the stay and myself.

We installed a camp (Figure IV.5) on the border of the camping area rented by the VOI and used by the DBCAM. This area is situated at the entrance of the village, and my local team could get back to their respective home every night. Weekly provisioning was guaranteed by the products available in the weekly local market and I organized one additional substantive provisioning by car in the middle of the stay.

2. On the look for mongoose lemurs

We started to look for *E. mongoz* on May 15th using several methods, first, we walked around the roads and few transects crossing different parts of the forest at dawn and dusk, We also carried out some playbacks of *E. mongoz* calls provided ahead by my colleague Dr. Matthias Markolf, postdoc researcher in the Sociobiology/Anthropology department of the University of Göttingen. These playbacks were unsuccessful, with only a few answers from the *E. fulvus* and none from *E. mongoz*. More successfully, our guides interviewed some villagers on possible places and times they had encountered the *E. mongoz* in the past and adapted our walks in accordance.

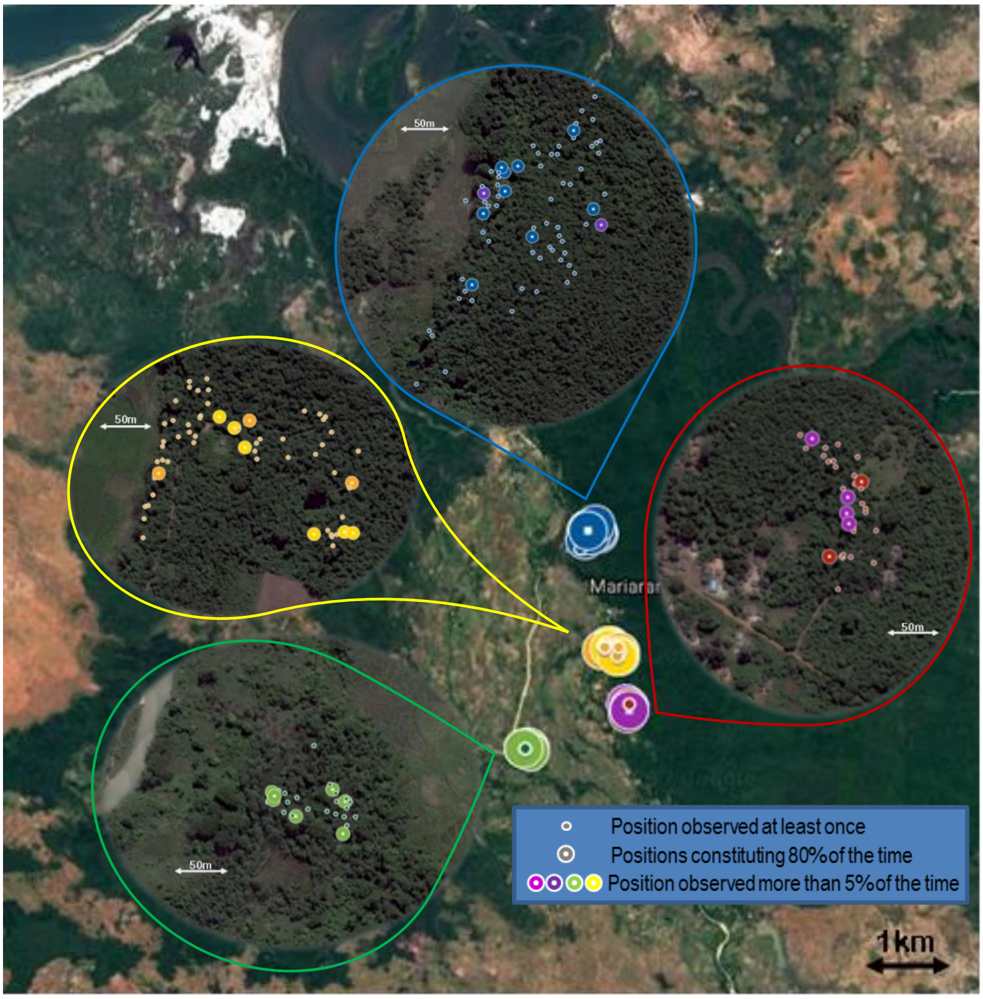


Figure IV.6: Space occupation by the different groups identified in Ankatsabe forest

We found our first group on May 17th, only three days after starting to look for them. This group was a couple found at the border of our camping area (red in Figure IV.6). We then found, 9 days later, on May 26th, a solitary male in an isolated fragment of the forest (green in Figure IV.6). On June 4th, we found a group of 4 individuals, an adult pair, and likely their two female offspring from the two precedent years (blue in Figure IV.6). We finally found our last group on July 3rd; this group had the same composition as the precedent one (yellow in Figure IV.6). Figure IV.6 shows the space occupancy of these different groups during our study time. Figure IV.7 shows the frequencies at which the different groups could be located. On average 75.2% (n=149) of our visits were successful, meaning that we could localize the individuals. These individuals were observed during their daytime activities between 6 am and 10 am and then between 3 pm and 6 pm. Once arrived in a given territory, the individuals were on average located after 1.2±0.2 hours of research. Hence, to maximize observation time we always left camp two hours before the observation time started.

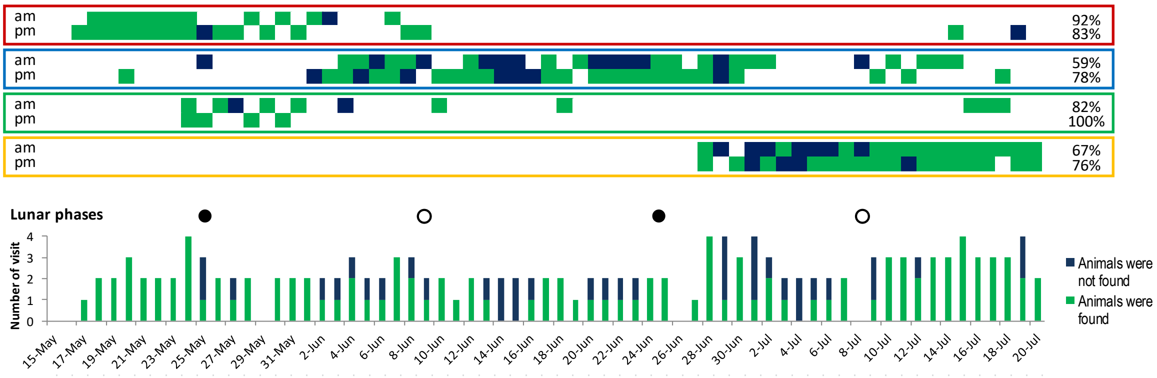


Figure IV.7: Localisation frequencies of the different groups of E. mongoz identified in Ankatsabe forest.

Individual recognition was possible and facilitated by sexual dimorphism, special features (walleyes, one-eyed), size, and color patterns. A few days' live observation training and through pictures was enough to recognize the individuals accurately. After 2-3 visits, the individuals stopped spending considerable time staring at us and no more occurrences of alarm vocalizations or tail waving were observed in our direction.

Figure IV.8: Trap for ground birds found in Ankatsabe forest

Figure IV.9: Wild boar hunted in the border of Ankatsabe forest

Building on the experience in Mahaitromby and following the recommendations of (Williamson and Feistner 2003) I decided to provide special tee-shirts for our observations. The idea is to provide additional cues to the animals allowing them to identify us and possibly discriminate us from other humans as potential hunters. The color blue was chosen considering the knowledge on color vision in true lemurs (Jacobs and Bradley 2016) and to respect the "fady" of certain ethnic groups in Madagascar. During our stay, we found traps for ground birds on one occasion (Figure IV.8) and toy weapons to hunt lemurs in the forest. We also heard some mention of hunting events but mostly happening outside of the area managed by the VOI. We also witnessed one wild boar hunting event (Figure IV.9). This event was justified to us by being outside the protected area, the wild boar having been found and hunted in the border of the rice fields.

Figure IV.10: Forest burning activity for village extension observed in Mariarano

During my time in Mariarano I could witness some cleared forest areas in the border of the forest (Figure IV.10). These areas were likely intended to answer the village expansion with new buildings and houses construction. One of these open areas even seemed to have cut the territory of one of the groups we observed as they were observed in both extremities of this open area. However, I also observed some well-preserved forest areas and active and strong engagement of part of the local population to preserve the forest.

IV. Conclusion

This report aims to share knowledge and information on possible sites to study *E. mongoz* and forest degradation. It is also a testimony of my own learning process on organizing projects, take decisions, and manage a team and a budget. It is probably, even more, a testimony of my discovery of the ethical responsibilities that go hand in hand with any research project independently of possible conservation ambition. This is especially true when approaching unhabituated populations of critically endangered species. I feel privileged to have spent a bit of time with these wild and rare individuals and hope to contribute somehow to increase the knowledge I have about them. I feel just as privileged to have shared this time with welcoming, experienced, passionate, and open-minded people from the local community. This experience was as challenging as inspiring both professionally and personally.

V. Acknowledgments

I am first extremely grateful to LLuìs Socias Martìnez for believing in this project by my side, for his resulting continuous support during this long and absorbing process, and his understanding. I also particularly and warmly thank Basile Andriambeloson, Janoarisaona Randrihaniharisoa, Armand-Célestin Tsimanihitra, Lydia Raharisoa, and Mônique Rayanadramiasy for their welcome, their guidance, and participation during daily life and data collection in Mariarano. They were great and indispensable support in this adventure and will remain as a family. I am also grateful to Claudia Fichtel and Peter Kappeler for their trust and for believing in and supporting this project. I also thank Lilas Allard for her active participation in data collection. I also thank the VOI members of Mariarano village, the DBCAM (Development and Biodiversity Conservation Action for Madagascar) members, and Rodin Rasoloarison for their contribution to implementing the research site and making this research possible. I thank Nourdine Mohamed for his welcome and guidance during the Mahaitromby expedition. I also acknowledge Solofonirina Rasoloharijaona, Herimalala Raveloson, Radhika Dave, Barry Ferguson, Peter Long, Rindra, Sam The Seing, Matthias Markolf, Jennifer Pastorini, and Steve Goodman for answering my questions and sharing their experience, making this camp installation possible. I thank the Malagasy Ministère de l’Environnement et des Eaux et Forêts and the Direction Générale de l’Environnement, de l’Ecologie et des Forêts de la région de Boeny to allow this research. This research was conducted with the research authorization number 71/17/MEEF/SG/DGF/DSAP/SCB.Re and was funded by the Deutsche Forschungsgemeinschaft (DFG FI 929/13-1) and the German Primate Center.

Chapter V: Remotely releasable collar mechanism for medium-sized mammals: an affordable technology to avoid multiple captures

A paper in Wildlife Biology (published on October 3rd 2019)

With Jeroen Buil, Matthias Dörge, Claudia Fichtel, Peter M. Kappeler and Hansjörg Scherberger

***** Jeroen Buil and Louise Peckre contributed equally to this paper.

Contributions (following CRediT taxonomy): Conceptualization, L.R.P., C.F, and P.M.K.; Methodology, J.B., and L.R.P.; Investigation, J.B., and L.R.P.; Resources, C.F, P.M.K. and H.J.; Writing – original draft preparation, J.B., and L.R.P.; Writing – review and editing, J.B., L.R.P, C.F., P.M.K., and H.S.; Visualization, J.B..; Supervision, C.F., P.M.K.and H.S.; Funding acquisition, H.S.

Abstract – Collar-mounted monitoring devices for collecting behavioral or positional data (e.g., sound recorders, accelerometers, GPS, VHF) are increasingly used in wildlife research. Although these tools represent an improvement in terms of data quality, they require capturing animals. Using remotely releasable collars allows for reducing the number of captures by half; however, currently this technology is primarily available for large mammals. Here, we present a locking mechanism design that is remotely releasable and light enough (22 g) for medium-sized mammals (>1 kg), can run in low-power mode for years, is reusable directly after recharge, and has a material cost of less than €50. An Android application operates this mechanism over a Bluetooth connection. We developed custom-purpose software for both the locking mechanism and the Android application. We tested two collars equipped with this locking mechanism in field-like conditions on two ring-tailed lemurs *Lemur catta*. The release mechanism has an operational range of 10–50 m and can run in active mode (allowing remote release) for several hours. Implementation of the presented release mechanism for collars on medium-sized mammals provides a low-cost solution to reduce the number of captures. We demonstrate that some low-cost technical improvements of tools used for studying wildlife can have significant effects on reducing the stress experienced by animals during capture. Detailed description of this new mechanism design provides a starting-block for potential adaptations for a broader range of species.

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General Discussion and Conclusions

While the current formulation of the SCHCC offers a vast concept, specific links between one social factor and one specific communicative variable are mostly tested independently, oversimplifying the relationship between social and communicative complexity. Moreover, despite these tests being carried on specific variables, their results are usually interpreted at the level of the broad framework providing a poor understanding of the underlying mechanisms of the observed relationship between social and communicative complexity. Hence, throughout this manuscript, I argue for the importance of expanding the tests of the SCHCC by combining both, 1) a more comprehensive approach of communicative complexity at the system level and 2) formalize and test more specific predictions associated with the SCHCC.

I believe that these two approaches nicely complement each other in contributing to render a clearer picture of the interactions between social and communicative complexity. They allow integrating phylogenetic and functional questions in order to help elucidate the specific selective pressures at play in the observed relationships between social and communicative complexity. They also allow addressing the current gaps associated with the tests of the SCHCC that I identified and described in chapter I. In the following sections, I develop and discuss how these approaches and the results of their applications in the present manuscript contribute to addressing these weaknesses. I finally discuss further perspectives on how these approaches may additionally provide essential insights into numerous related current fascinating debates on the evolution of social cognition and language.

I. Developing better operational definitions of communicative complexity

1. Accounting for the multimodal nature of communication

The ongoing debate on how to best quantify social complexity recently highlighted the necessity for a more comprehensive approach instead of the usage of a single proxy to avoid dismissing essential aspects of sociality (Kappeler 2019; Hobson et al. 2019; Roberts and Roberts 2020; Prox and Farine 2020). Here I argue for the importance of adopting a similarly comprehensive approach to communicative complexity taking into account the multimodal nature of communication. I offer a new analytical framework to assess communicative complexity across modalities. This framework was developed among two axes. The first axis focused on establishing measures that can be implemented across modalities (e.g., number of signals, signaling rates). In chapter I (section II.2), I provided a detailed description of the current applications of these measures in the three modalities dominating the current literature (i.e., acoustic, visual, and olfactory). The second axis focused on determining measures that can describe the communicative system more holistically, including signals across different modalities (e.g., degeneracy, modularity). These measures are described in chapter I (section II.3). In chapter II, I applied this proposed framework to two true lemur species differing in their social systems. This framework allowed to reveal differences both at the signal and system levels between these two species. These differences were coherent with the predictions drawn based on the SCHCC as *E. rufifrons*, the species having the more complex social system, also had overall a more complex communicative system than the one of the *E. mongoz*. As far as I am aware, chapter II provides the first quantitative description of the complexity of a communicative system across modalities.

2. Broadly applicable measures to ease cross-taxonomic comparisons

Besides, this cross-modal approach, I additionally conceived this framework with the idea of providing measures applicable to a broad range of taxa. This is, by all means, challenging, and only future tests will unveil its relevance and applicability. But, if the applicability and relevance of this framework at the inter-taxonomic level remain tentative, I, nevertheless, discuss in chapter II (section IV.7) some predictions on how different social systems may impact the proposed measures of degeneracy and modularity. I also offer in Figure II.12 (chapter II) a visualization of the space of communicative complexity defined by these two measures and how signaling networks may look like when moving across this space. This framework may and should evolve through confrontations to different taxa and discussions across taxa specialists. I nevertheless hope to have put some light throughout this manuscript on the importance and interest of such a broadly applicable comprehensive approach. I also hope that this may encourage researchers to fill the gaps, for instance, on insect social and communicative systems (Leonhardt et al. 2016; Nehring and Steiger 2018).

3. Clarifying the level at which complexity is evaluated

Recent studies highlighted the fundamental importance of clarifying the scale on which analyses or measures are made (Aureli and Schino 2019; Kappeler 2019; Peckre et al. 2019;

Hobson et al. 2019). Current tests of the SCHCC include species, group, and individual properties as well as dyadic and specific social interactions. It is especially important to clarify the evaluated scale because, as I discussed in the general introduction and chapter II, individuals and species, for instance, may face different levels of complexity. For example, certain social systems may require communicative complexity at the individual level, each individual being required to convey information across a variety of contexts. On the contrary, other social systems may favor social roles with a single individual being exposed to a more limited range of contexts, hence facing a reduced need for communicative complexity (Leonhardt et al. 2016; Lucas et al. 2018). Here, I argue that both a more comprehensive approach of communicative complexity at the system level and the formalization of more specific predictions associated with the SCHCC would force researchers to address this question.

4. Difficulty and importance of defining a clear framework

As definitions vary and vary even more across researchers working in different modalities and different taxonomic groups, an essential effort for dissipating dissimilarities in the approach is necessary. It is only on that condition that the framework I offer here would make complete sense. Measures of signaling network degeneracy and modularity discussed in chapters I and II are necessarily impacted by the way we defined signals, as this choice of definition will impact the number and nature of the nodes in the signaling network. If the impact is probably reduced when comparing species with relatively similar communicative systems as true lemurs, it may have a more significant impact when comparing the complexity levels of more divergent signaling systems. I also provide in chapter II, two comparative approaches (i.e., rarefaction analysis and distribution of the differences between values of null models) that should also account for some variability in the definitions. Dissipating these definitional dissimilarities is probably a long way to go of intense exchanges, but I hope it would be a stimulating one. Below I address some specific definitional issues, try to clarify my current position, and what I believe are the most important weaknesses of my framework regarding these.

a. Our definition of signal

Etymologically, the term “signal” refers to a “visible sign”, an “indication”, something “distinguished from what is ordinary” (Harper 2001b). However, traditionally, the field of animal communication has made a distinction between signals and cues (Maynard-Smith and Harper 2003; Leonhardt et al. 2016; Freeberg et al. 2019). Signals are features of the sender that communicate something to a receiver and that have evolved for that communication purpose. Whereas cues communicate something to a receiver as an incidental by-product but are generated either inadvertently or for a purpose different than communicating information. When the receiver responds to a cue and the emitter benefits from this response, then this cue may evolve into a reliable signal. Despite this classification, many actions performed by animals cannot be easily assigned to one of these discrete categories as they may have both signaling and non-signaling functions (Bradbury and Vehrencamp 2011). For instance, cuticular hydrocarbons, besides carrying multiple pieces of information, are essential to protect insects against desiccation and pathogens (Leonhardt et al. 2016). Moreover, from the perspective of the receiver, and in the context of navigating a social environment, individuals also benefit from being able to monitor cues of their conspecifics that can be used to predict future actions (Bradbury and Vehrencamp 2011). Hence, here I use a rather broad approach to communication incorporating signals and cues under the general term "signal" or "signaling unit". For instance, while describing the communicative system of both true lemur species in chapter II, I included yawn and self-grooming as signals.

b. Meaning, structure, and context of usage

Several authors have proposed a distinction between the message (information) sent by a sender and its meaning, extracted by the receiver (Kershenbaum et al. 2014; Liebal and Oña 2018). Meaning is then inferred from the presence of a predictable response from the receiver. This approach is commonly used in acoustic and olfactory studies, notably through the use of playback experiments (Liebal and Oña 2018). Studies on visual signals focus instead on the signaler behavior and investigate whether the individual communicates in a goal-directed way employing voluntarily controlled actions (i.e., intentionality) (Liebal and Oña 2018). An additional distinction is made between the broadcast information (i.e., content) and the transmitted information (i.e., efficiency) (Hebets and Papaj 2005; Kershenbaum et al. 2014). The broadcast information may then only refer to the form or structure of the signal. It refers to the inherent properties of signals, that does not necessarily have meaning per se, and do not refer to the putative behavioral effects on receivers, or the ultimate evolutionary processes associated (Kershenbaum et al. 2014). In the context of the SCHCC, as mentioned in chapter I (section I.2.b), I argue that considering the social information contained in signals, rather than the possibilities offered by the structure of these signals to convey flexible and diverse information as a measure of communicative complexity, may lead to non-informative tests of the SCHCC. I rather use an approach based on information theory, which represents a measure of the entropy of a system, that is, an estimate of the amount of uncertainty (Shannon and

Weaver 1949; Robinson 2008; Cuthill et al. 2017; Fischer et al. 2017b). I do not put my focus on measuring what one communicates, but rather on measuring what one could communicate.

Signals are also considered to vary in association with internal (hormonal, motivational, emotional) and external (location, presence of another individual, threat detection, presence of a resource) factors (Kershenbaum et al. 2014). These contextual factors are of essential importance to determine the meaning of a signal, as they also influence its perception and the costs and benefits associated with the response. Hence, many researchers also address the functional question of signals by assessing their degree of production specificity, their degree of response specificity, and their contextual independence. Here I choose to distinguish signals based on their structure and not on their context of emission. In a recent study, Hammerschmidt and Fischer (2019) found a similar number of call types across three baboon species based on their acoustic properties but mentioned that if the distinction had been based on the context of usage, the conclusion would probably have been different. This approach was also recently encouraged by Crockford (2019) in chimpanzees, where major call types could be identified across different chimpanzee subspecies and populations but where a classification based on the context of usage led to much more variability in the definition of these different call types.

A difficulty arises, notwithstanding, when choosing an approach based on the structure of the signal and ignoring its contextual use as the one used in my project. We may indeed be more prone to define signaling units and calculate measures that do not have biological meaning because of being too broad or too narrow compared to what the organisms themselves can perceive (Hobson et al. 2019). Here is another situation where I see the relevance of combining a comprehensive approach to more specific tests of the SCHCC as further tests on the specific function of derived and complex signals appear essential to complement the picture in this context.

c. *Signaling unit: where are the boundaries?*

Moreover, once agreed on defining signals based on their structure, we are not out of the woods yet. Indeed, considering the acoustic modality, for instance, there is no single definition of an acoustic unit or a call type (Kershenbaum et al. 2014; Fischer et al. 2017b; Anikin et al. 2018). As Kershenbaum and colleagues (2014) described, units can be delimited either by silence or by a radical change in signal properties; on the contrary, several sounds may be grouped as a unit if they are repeated or always simultaneously produced. This issue is even more pronounced when looking across modalities. Multimodal signals have been classified as either fixed signals where the two modalities are necessarily combined due to the mechanics of signal production or fluid signals where each component may be produced separately (Partan and Marler 1999). Here I considered fixed signals as one signal while each component of a fluid signal was considered separately if these were not always produced together. For instance, in chapter II, anogenital scent-marking was considered as one signaling unit, whereas flick-tongue and grunt were considered as two distinct signaling units since, even if often produced together, they were also sometimes produced separately. This logic was also applied to signals within a given modality. Hence, if two call types occurred without being separated by silence, I considered them as separate signaling units if they were sometimes produced separately.

5. Can we avoid circularity?

An important additional issue discussed earlier in chapter I (section II), and chapter II (section IV.7) is the issue of circularity that occurs similarly between sociality and cognition (Bergman and Beehner 2015) and sociality and communication (Kappeler 2019; Peckre et al. 2019). If social complexity is measured through communicative interactions or communicative complexity, then positive correlations are expected but may not reveal the mechanism we aimed to highlight. This consideration is another justification for my choice of considering signals based on their structure and not on their contextual use (see section I.4 above). Additionally, in the framework introduced in the present work, I also choose not to consider as signals behaviors that are usually considered to assess social relationships, such as approaches, grooming, body contact, and aggressions (Bergman and Beehner 2015; Fischer et al. 2017a). Bergman and Beehner (2015) also suggested measuring social cognition in a different context than the chosen measure of social complexity. Another perspective would be to include the previously mentioned behaviors as communicative signals in our appreciation of communicative complexity and only use measures of social complexity based on social organization, excluding, therefore, the circularity with measures of social structure. However, this approach can and has been criticized on the grounds that measures of social organization (notably group size) alone do not fully capture all relevant dimensions of social complexity (Shultz and Dunbar 2010; Kappeler 2019).

II. Sociality and communication complexity: understanding causality

As discussed in chapter I (section III.1), correlative studies do not permit conclusions about the direction of causality. This is why, rightly, some studies also proposed that instead of complex communicative systems evolving in response to pressures related to social complexity, complex communicative systems might have facilitated the evolution of greater social complexity. In chapters II **and** III, I side with the idea that if complex communication is the prerequisite to social complexity, hence, at first, other selective pressures are responsible for the evolution of this complex communication. By choosing to compare two closely related species, having similar morphology and ecology, and living in similar habitats, I hope to limit the number of these potential alternative selective pressures that may have selected for more complex communicative systems. Phylogenetic history, anatomy, and ecology are indeed all factors that have been shown to influence a species communicative system. Such comparisons are rare as most previous studies focused on closely related species, which widely differ in their habitat type, ecology, and/or morphology. For instance, Gustison and colleagues (2012) compared two closely related species with different social systems (chacma baboons, *Papio ursinus*, and geladas, *Theropithecus gelada*) and interpreted the presence of a derived call in geladas as a result of additional social pressures due to long-term cross-sexual bonding in this species. Hammerschmidt and Fischer (2019) recently compared the vocal repertoire of chacma (*Papio ursinus*), olive (*P. anubis*), and Guinea (*P. papio*) baboons and suggested that the derived call observed by Gustison and colleagues may rather find its origins in selective pressures associated with their ecology. Hence, I argue here for the essential importance of mentioning and discussing these differences when testing for the SCHCC. If comparisons of closely related species, having similar morphology and ecology seems to be an interesting perspective, the number of potential species comparisons fulfilling these conditions are largely limited. However, the spread of the implementation of new available methods allowing to control for alternative hypotheses or to better appreciate the causality in broader inter-specific comparisons may also largely contribute, in the foreseeable future, to a more accurate examination of the sequential order in which correlated variables appeared in the evolution (Dunbar and Shultz 2017).

III. Better understand the underlying mechanisms: exploring the relationship(s) between signal variation and social factors

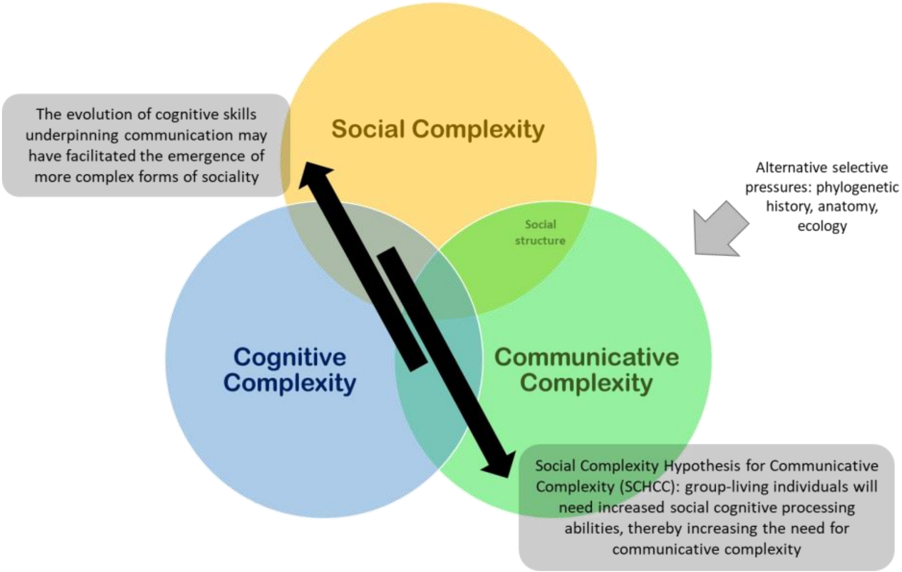
Although several studies have supported the SCHCC by revealing correlative relationships between specific social and communicative variables, both the direction of causality and the mechanisms underlying these links remain currently unclear (Freeberg et al. 2012a; Gustison et al. 2012, 2016, 2019). Hence, in this manuscript, I call upon formalizing and testing more specific predictions associated with the SCHCC. Developing more specific predictions of the SCHCC focusing on specific relationships between one social variable and one communicative variable, with a clear formulation of a hypothesis explaining the mechanism linking these two variables, may also contribute to clarifying the direction of this link. In chapter I (section III.2), I offer suggestions on how to explore the nature of the relationship between social and communicative complexity through more specific predictions both at the ultimate and proximate levels.

First, I emphasize the relevance, when comparing closely related species, of identifying the signals that are not shared in the repertoires. These signals may be newly derived signals or be more ancestral but conserved in some species and not the others. These non-shared signals are the ones that may have been the result of different evolutionary pressures. Studying their social functions and assess their potential fitness consequences in detail will help to identify the potential social selective factors driving their evolution (Gustison et al. 2012; Liebal et al. 2013; Wadewitz et al. 2015; Fischer et al. 2017b). In chapter II, I identify several non-homologous signals between the mongoose lemurs and the red-fronted lemurs and discuss their known context of usage. I observed two main tendencies, with an increased communicative complexity associated with social interactions in red-fronted lemurs compared to mongoose lemurs and an increased communicative complexity associated with disturbance in mongoose lemurs compared to red-fronted lemurs. Moreover, this analysis also allows us to identify some signals for which there is a particular interest in studying their function in more detail (e.g., flick tongue, anogenital scent-marking, plurr call). Indeed, conceptualizing communicative complexity along multiple axes and scales may help to generate more accurate predictions about which specific social parameters may be responsible for the selection of new or more complex signals. Hence, besides fostering the interest and necessity of a comprehensive approach per se, I believe that such an approach is also an interesting ground to formulate and test more specific hypotheses and predictions in the context of the SCHCC.

In chapter III, I also offer an application of a suggestion proposed in chapter I (section III.2.b) on a possible way to explore the nature of the relationship between social and communicative complexity at a proximate level. I propose that the SCHCC could provide a theoretical framework for testing audience effects by considering variation in the audience as an aspect of social complexity. I argue that studying audience effects on complex signals may help to uncover particular social selective pressures that may have led to the evolution of flexible signals. In chapter III, I investigated the existence of potential intragroup audience effects on anogenital scent-marking behaviors in red-fronted lemurs. I particularly investigated whether males and females differed in this aspect and if these differences may reveal functional differences associated with anogenital scent-marking across sexes. I found an intragroup audience effect in males but not in females in agreement with the idea of a greater level of intragroup social pressures associated with anogenital scent-marking in males than in females in an egalitarian lemur species. However, in my observations, anogenital scent-marking seemed to be increased in males in the absence of other males. This fact goes against the demonstrative marking hypothesis. Hence the social pressures at play between males do not seem to be at the origin of the multimodal nature of these signals but may have rather constituted pressures to adopt certain behavioral flexibility.

IV. The sociality-cognition-communication complex

Social, cognitive, and communicative variables appear to be deeply intertwined (Figure 1 in the general introduction, Figure 2). Communication is even sometimes considered a defining part of social complexity. In this way, Kappeler (2019) describes communication as a core constituent of a species' social structure. This consideration emphasizes all the more the importance of considering circularities issues when defining the communicative variable we want to use (section I.5). Cognition is usually described as a middleman between social complexity and communicative complexity. However, while the SCHCC suggests that social complexity will require the need for increased social cognitive processing abilities, thereby increasing the need for communicative complexity (Figure 1 in the general introduction, Figure 2), other authors suggest that the evolution of cognitive skills underpinning communication complexity may have facilitated the emergence of more complex forms of sociality (Figure 2; McComb and Semple 2005; Freeberg et al. 2012a, 2019; Dunbar and Shultz 2017; Roberts and Roberts 2020). The development of the latest idea, explains why there is a growing body of literature arguing for a better consideration of communication when looking at the evolution of social cognition (Searcy 2019; Freeberg et al. 2019; Roberts and Roberts 2020). As I argue for the link between social and communicative complexity, the specific nature of the links between social complexity and cognitive complexity and between cognitive complexity and communicative complexity remain poorly understood (Roberts and Roberts 2020). In sum, if social, communicative, and cognitive complexity seems to be highly interlinked, We are just at the beginning of understanding the underlying mechanisms at play. Studies on the evolution of social complexity, cognitive complexity, and communicative complexity should all benefit from formulating clear hypotheses on the chain of consequences linking these different aspects. Hence, I believe that expanding the tests of the SCHCC in the two directions pointed out in this work (i.e., comprehensive approach and formalization of more specific predictions) would necessarily contribute to clarify the nature and direction of causality of the interrelations underpinning the sociality-cognition-communication complex.



The evolution of cognitive skills underpinning communication may have facilitated the emergence of more complex forms of sociality

Alternative selective pressures: phylogenetic history, anatomy, ecology

Social Complexity Hypothesis for Communicative Complexity (SCHCC): group-living individuals will need increased social cognitive processing abilities, thereby increasing the need for communicative complexity

Figure 2: The Sociality-Cognition-Communication complex

V. How can my work contribute (or not) to understanding the evolution of language?

In 1972 Bateson raised the question of the adaptative function of language. The vocal flexibility associated with language in humans did not replace the phylogenetically older neural network responsible for the production of non-linguistic vocalizations (Anikin et al. 2018). Hence, Bateson argued that language does not only serve a general communicative function, already fulfilled by the still-existent non-linguistic communication in humans, but that evolved under additional specific selective pressures. Dunbar’s vocal grooming hypothesis appears as an answer to this question of the adaptative function of language raised by Bateson (Leavens et al. 2014). Language may have evolved to serve social relationships once grooming, the conventional social bonding behavior in primates, became unable to serve this function in larger groups (Dunbar 1998, 2003). Social interactions between long-lived individuals repeatedly interacting over time and forming long-term bonds, as found in many primate species, seem to be indeed a pivotal element to explain the evolutionary transition from non-linguistic communication to language (Cheney and Seyfarth 2018). If many primate vocalizations are highly genetically constrained, there exist many variations between species, hence several authors argue that studying the factors that originated these divergences may help to uncover the selective pressures that promoted vocal learning and flexibility in our ancestors (Cheney and Seyfarth 2018; Hammerschmidt and Fischer 2019; Blue 2020). In particular, flexible call usage associated with increasingly elaborated vocalizations to solve social challenges, communicate intentions and reduce ambiguity and uncertainty in social groups may have set the stage and created selection pressures leading to the evolution of learned flexible vocal production (Cheney and Seyfarth 2018). More broadly, many authors argue for the central importance of comparative data on communication and cognition in non-human animals for future progress on elucidating language evolution (Searcy 2019). Interestingly communication remains overlooked in strepsirrhines; this is quite surprising in this context as they are at the base of the primate tree and combine rich multimodal communicative systems with complex and diverse social systems. Here I described the communicative system of two true lemur species, providing a basis to further explore these questions. Especially, *E. rufifrons* seem to produce complex and diverse call sequences and assemblages. Network analysis is a well-established tool in the analysis of syntactical rules; hence my data could also provide interesting comparative data (Weiss et al. 2014). Additionally, playback experiments may reveal how much these sequences may be interpreted as hierarchical syntax (Suzuki et al. 2018; Prat 2019).

Moreover, as we have seen in the general introduction, more recent theories have focused on other modalities besides the auditory one, as the visual one (i.e., gestures) or a combination of different modalities (e.g., acoustic and visual) as potential precursors for language evolution. For instance, some researchers have looked at facial communication and have shown that lip-smacking, a common form of primate facial movement, is produced with a periodicity that closely matches the periodicity of the gaps between syllables in many human languages. They, therefore, suggested that lip-smacking may be an evolutionary precursor to speech (Chandrasekaran et al. 2009; Ghazanfar 2013; Bergman 2013). More recently, Lameira and colleagues (2015) have shown that other facial movements, "clicks" and "faux-speech", involving lips and tongue, are also produced at speech-like rates in orangutans. Interestingly, *E. rufifrons* exhibit flick-tongue signals that consist of the repetition of tongue extension from a nearly-closed mouth; this signal is commonly combined with a grunt vocalization and may constitute an interesting behavior to study under this context.

In addition to providing in chapter II data and perspectives for comparative analysis on multimodal communication in primates, in chapter I (section III.2.c) I also tackle the question of vocal production learning, another candidate for singling out human language from other animal communication (Hauser 2002; Fitch 2017; Prat 2019). Vocal production learning refers to the modification in the structure of vocal signals through experience with another conspecific (Janik and Slater 2000; Ruch et al. 2018). To date, the capacity of lexical learning (acquisition of new vocalizations) was only observed in a restricted number of species across the animal kingdom. Here I argue that more elaborated vocal behavior and babbling-like behavior might be more common in species with more complex forms of parental care, including allocare. Recent frameworks are taking increased awareness of the potential role of parental care evolution on the evolution of social systems (Kappeler 2019; Socias-Martínez and Kappeler 2019). Thus, I believe that studying the caring system in species in which flexible vocal learning takes place is first, a promising way to illuminate some causal relationships between social variables and communicative complexity, and second, an interesting framework to study potential language precursors.

However, I do not want to oversell my framework, and here only offer speculations on potential research perspectives. The contribution of comparative data on communication complexity for the understanding of human language evolution is still debated (Fischer et al. 2017b), and as pointed out in the general introduction a necessary effort first needs to be carried to homogenize the methods used in humans and other animals (Prat 2019). In this sense, the framework I offer to characterize communicative complexity may still be difficult to apply to human language, as it may be challenging to identify appropriate specific signaling units. However, network analyses are commonly used in research on human communication, based on distinct words (Ke and Yao 2008; Cong and Liu 2014). Moreover, Anikin and colleagues (2018) were recently the first to establish a repertoire of human non-linguistic vocalizations. Hence some hope may be given for future studies to bridge the gap between the research approaches used to study communication in humans and non-human animals.

VI. Looking across fields for mutual benefits

We earlier argued that the different approaches used to study different modalities might be put to build a common framework by complementing each other. I similarly argue for the importance of looking across research fields. Interesting parallels may be observed between animal behavior and linguistic research when addressing the question of the link between sociality and communicative complexity. Indeed, in linguistics, the similar three issues outlined in chapter I have also been mentioned. First, while speaker population size is the main proxy used for social complexity, its relevance is questioned (Nettle 2012). Second, difficulty to control for alternative hypotheses, as the environment or economic factors are also highlighted, especially as much fewer methods have been developed to take into account the historical relatedness existing between different languages than the phylogeny between different species (Nettle 2012). Finally, if as outlined in the introduction arguments for a link between sociality and the evolution of more complex communicative systems were for long mentioned in the literature, in linguistics as in animal communication, the nature of the underlying mechanisms remains largely unexplored. Theoretical hypotheses on the mechanisms by which social transmission may affect the cultural evolution of linguistic systems or on how social context could affect linguistic structure surged only relatively recently (Nettle 2012). These striking parallels between the problem encountered in these two disciplines lead me to believe that these two fields may benefit each other by exploring ways to cross-foster their approaches. This is already apparent with the recent increase in occasions to exchange across these two fields as the EVOLANG conference integrating non-human animal communication as a full section or the recent workshops “Animal linguistics: take the leap!” (2019) or “Teaching Exchange of Animal Linguistics” organized this spring in Paris (but canceled due to the corona crisis). With this work, I hope to have further encouraged these exchanges and bring insights into the current commonalities and differences existing between the two fields when addressing the SCHCC. By developing a framework of measures to characterize communicative complexity that I think applicable across a broad range of taxa, discussing some related definitional issues, and emphasizing the importance of homogenizing the methods used to study human and non-human animals communication, I hope to provide some baseline to develop further work in this perspective.

VII. A final note on ethical considerations

As in any research project, many ethical questions arose during the development process of this thesis project. Because I consider that addressing these questions is an essential part of the development of any research project, I here come back briefly to these questions. In my case, ethical issues arose in particular concerning two aspects: the choice of an appropriate field site to study *E. mongoz* and the use of technology, here collar-mounted recorders.

In chapter III, I share my experience and my knowledge about possible sites to study *E. mongoz* and report the state of forest degradation at the time of our visits. This report first aims to help potential future researchers interested in studying *E. mongoz* to identify an appropriate field site. Second, it may hopefully contribute to raising awareness on the importance of considering the consequences of habituation when choosing a field site and the importance of engaging the local community.

In chapter V, I provide the result of a three years reflection on how to combine best the use of technology and my ethical responsibilities for animal welfare. If the time required to develop a releasable collar prevented us from implementing the use of onboard attached recorders, we are happy to have been able to provide a detailed description of this new device, providing a starting-block for potential adaptations for other species and studies. I show that some low-cost technical improvements of tools used for studying wildlife can have significant effects on reducing the stress experienced by animals during capture. As a result, I hope to encourage researchers to think more often about the relevance and importance of such additional technology.

As mentioned in chapter IV, these take-home messages are first and foremost, a testimony of my own growing process regarding the importance of addressing the ethical responsibilities that go hand in hand with any research project.

Supplementary chapter (side project): Potential self-medication using millipede secretions in red-fronted lemurs: combining anointment and ingestion for a joint action against gastrointestinal parasites?

A paper published in Primates on July 30th 2018

With Charlotte Defolie, Peter M. Kappeler and Claudia Fichtel

Contributions (following CRediT taxonomy): Conceptualization, L.R.P.; Investigation, L.R.P., and C.D..; Writing – original draft preparation, L.R.P.; Writing – review and editing, L.R.P, C.D., C.F., and P.M.K.; Visualization, L.R.P.; Supervision, C.F., and P.M.K.; Funding acquisition, L.R.P., C.F, and P.M.K.

Abstract – Self-anointing, referring to the behavior of rubbing a material object or foreign substance over different parts of the body, has been observed in several vertebrate species, including primates. Several functions, such as detoxifying a rich food source, social communication and protection against ectoparasites, have been proposed to explain this behavior. Here, we report observations of six wild red-fronted lemurs (*Eulemur rufifrons*) of both sexes and different age classes anointing their perianal-genital areas and tails with chewed millipedes. Several individuals also ingested millipedes after prolonged chewing. In light of the features of the observed interactions with millipedes, and the nature and potential metabolic pathways of the released chemicals, we suggest a potential self-medicative function. Specifically, we propose that anointing combined with the ingestion of millipedes' benzoquinone secretions by red-fronted lemurs may act in a complementary fashion against gastrointestinal parasite infections, and more specifically Oxyuridae nematodes, providing both prophylactic and therapeutic effects.

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