# UNIVERSIDAD COMPLUTENSE DE MADRID
## FACULTAD DE CIENCIAS BIOLÓGICAS

## TESIS DOCTORAL

# A comparative study of sociality and prosociality in geladas, *Theropithecus gelada*, and mandrills, *Mandrillus Sphinx*

Estudio comparado de la socialidad y prosocialidad en geladas *Theropithecusm gelada*, y en mandriles, *Mandrillus Sphinx*

MEMORIA PARA OPTAR AL GRADO DE DOCTORA

PRESENTADA POR

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UNIVERSIDAD COMPLUTENSE DE MADRID
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# A COMPARATIVE STUDY OF SOCIALITY AND PROSOCIALITY IN GELADAS, *THEROPITHECUS GELADA*, AND MANDRILLS, *MANDRILLUS SPHINX*

## ESTUDIO COMPARADO DE LA SOCIALIDAD Y LA PROSOCIALIDAD EN GELADAS, *THEROPITHECUS GELADA*, Y EN MANDRILES, *MANDRILLUS SPHINX*

TESIS DOCTORAL DE:

**LETICIA ORTEGA BALLESTEROS**

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**Tesis Doctoral 2017**

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Memoria presentada por Leticia Ortega Ballesteros para optar al grado de Doctor en Ciencias Biológicas, dirigida por el Doctor Fernando Colmenares Gil (Departamento de Psicobiología), de la Universidad Complutense de Madrid.

Madrid, 2017

| El Doctorando | Vº Bº del Director |
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| Leticia Ortega | |
| Leticia Ortega Ballesteros | Fernando Colmenares Gil |

*A mis padres*

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# INDEX

# SUMMARY

*Sociality* or *group living* has evolved independently in many animal taxa, but only in some of them it is based on *social bonds* between group members that are serviced through the exchange of a variety of social behaviours with multiple partners. This *bonded sociality* of nonhuman (and human) primates and of a few other taxa stands out for its reliance on *prosociality* or *cooperation* between individuals who typically know well one another and who engage in long-term, highly individualized partnerships. The patterns of sociality and prosociality observed in primates reflect *trade-offs* between several antagonistic but equally welfare- and fitness-enhancing activities and, ultimately, are the outcome of the way the individuals skilfully manage their inevitable *conflicts of interest* through strategies of *aggressive competition*, *cooperation* and *post-conflict reconciliation*. Contemporary theory on primate sociality and prosociality emphasizes the need for integrating *socio-ecology* (i.e., ecological, demographic and social factors), *phylogeny* (i.e., evolutionary history) and *life history* (i.e., life history traits) in any account of the *proximate* and *ultimate causes* of variation in primate social systems.

The present research was aimed to study sociality and prosociality in two groups of African papionins, the gelada (*Theropithecus gelada*) or montane baboon and the mandrill (*Mandrillus sphinx*) or forest baboon, housed in rather similarly naturalized, sized and vegetated enclosures in captivity. The study was largely theory-driven and was aimed to test several specific assumptions and predictions that were fully spelled out in three empirical chapters (chapters 2-4). The methodological approach adopted was observational and comparative. The general objectives of this research can be stated as follows:

1. To analyse the activity time budgets of two different species housed in similarly benign ecological conditions, that is, food-provisioned and predation free, and test two competing models regarding the activity budget categories that should be expected to increase (or decrease) when individuals are freed of ecological stress (chapter 2).

2. To carry out a fine-grained study of socio-spatial behaviour of the two species in terms of sociality (time spent accompanied *versus* alone) and gregariousness

(number of neighbours when accompanied) at four different social distance categories (chapter 2).

3. To test the prediction of the biological market theory that variation in a group's dominance gradient will influence the patterns of reciprocity and interchange of grooming and prosocial behaviour (i.e., punishment) (chapter 3).

4. To test the Covariation hypothesis prediction that the patterns of conflict management tend to be intercorrelated and are related to the group's dominance style and hierarchy steepness (chapter 4).

5. To test the prediction of the Relational model that individuals that have participated in an agonistic encounter are likely to switch their aggressive motivation to an affiliative mode and engage in affiliative behaviour right after the conflict has ended (chapter 4).

The study was conducted from October 2010 until April 2011at La Vallée des Singes, a large monkey and ape park located in Romagne (France). The subjects were the members of a group of 9 geladas, *Theropithecus gelada* and a group of 17 mandrills, *Mandrillus sphinx.* The enclosures were large (2,800 and 3,500m2) and vegetated and fully equipped with a variety of enrichment devices. The study involved the sampling and recording of (a) four general categories of *behavioural activity*, namely, *moving*, *foraging*/feeding, *resting* and *socializing*; the social activity category was further broken down into three subcategories, namely, *affiliation*, *aggression*, and *social play*; (b) four categories of *social distance*, namely, *contact*, *within one arm's reach*, *within two arms' reach* and *between two arms' reach and 4 meters*; and (c) a large repertoire of *assertive* [e.g., supplant, present], *agonistic* (aggressive [e.g., threat, hit] and submissive [e.g., bared teeth display, flee]), *affiliative* [e.g., groom], and *cooperative* [e.g., support and punish aggressors or victims] behaviours. These behavioural records were sampled via *focal-individual* and *focal-group sampling* techniques and collected via *time-point (or instantaneous) sampling* and *continuous recording* over a period of 22 weeks. The raw data were transformed into different behavioural measures that were then used to analyse the specific questions addressed in each of the three empirical chapters. The records on behavioural activities and socio-spatial behaviours were used to study *activity time budgets* and *sociality* and *gregariousness* (chapter 2), and the records on agonistic, affiliative and cooperative behaviours were used to study *dominance gradients* and *reciprocity* and *interchange* of *aggression*, *grooming* and *punishment* (chapter 3), and to study *dominance styles* and *conflict management strategies* (chapter 4).

The main findings and conclusions from this study can be summarized as follows:

1. Despite their living in an ecological setting free of predators and food-provisioned, the two study groups' activity budgets fell well within the range of variation of *activity budgets* that have been described for wild populations of gelada and *Papio* baboons that are ecologically stressed. This finding raises the question as to why in the highly benevolent ecological conditions that the two groups faced in captivity the individuals' activity time budgeting decisions appeared to be so resilient.

2. Although the two groups' overall activity budgets were similar, they were not identical. Both geladas and mandrills kept high levels of *foraging* time, however, the former kept higher levels of *social* than *moving* time, and the latter scored higher in *resting* than *social* time.

3. In both groups, the time spent in *affiliative behaviour* was far greater than that spent in *aggression*. This pattern has also been reported to occur in wild populations. These results lend support to the view that the relation between captivity and behaviour is far from simple. Within certain limits of ecological variation and in strongly socially evolved species, individuals appear to be more sensitive to the social and demographic characteristics of the socio-ecological niches they encounter in captivity than to other variables typically associated with captive settings.

4. The individuals from the two study groups were found to spend most of the time alone, i.e., without neighbours, within a radius of two arms' reach. This rather weak *sociality* was shared by both species; none the less, geladas scored higher than mandrills in sociality at all social distance categories analysed.

5. In both groups, the individuals' *gregariousness*, i.e., the number of neighbours found at the various categories of social distance, was found to be rather meagre. When they were accompanied within the radius of two arms' reach, they were hardly found with more than two partners. And at the farthest distance this pattern was not much different, either. As with sociality, geladas were also more gregarious than mandrills. This socio-spatial organization where individuals are mainly arranged in duos or trios is intriguing and raises important issues with regard to the nature of group cohesion and its behavioural, psychological, and socio-ecological underpinnings.

6. The dominance hierarchy of the mandrill group was steeper than that of the geladas'. Contrary to the predictions of the biological market theory, grooming was reciprocally exchanged regardless of variation in dominance gradient. In line with the expectations, there was a negative (unidirectional) interchange of grooming for punishment in the group with greater dominance gradient; however, this correlation was only marginally significant.

7. Dominance rank was generally found to be a good predictor of the distribution of dyadic and triadic aggression; however, it did not predict the distribution of affiliative (grooming) measures. This rank independency of grooming could explain why it was reciprocated for itself rather than interchanged for agonistic support or, in our study, the avoidance of punishment.

8. Grooming partnerships were found to be strongly related to time in spatial association (i.e., proximity partnerships). However, in several cases, the patterns of reciprocity and interchange found were independent of proximity. That is, individuals were found to give relatively more often of a given behaviour to those from whom they received relatively more often of that same (in reciprocity) or another behaviour (in interchange) in return. This meant that reciprocity or interchange was genuine and not a by-product of proximity.

9. As expected, aggression and victim-punishment, where the power differentials between the punishers and the targets were more elevated, were both unidirectional, a pattern that was stronger in the group with steeper dominance hierarchy. And, as expected, aggressor punishment was reciprocal in the group with smoother dominance gradient.

10. Aggressive interventions by third-parties tended to go down the hierarchy, which implies that they minimized risks of retaliation. However, in the more egalitarian group of geladas, some of the interventions were not 'conservative', but 'bridging', which means that interveners supported the lowest-ranking individual (i.e., the victim) against the middle-ranking opponent (i.e., the aggressor).

11. Aggression was interchanged for grooming. Since the study did not analyse short-term contingency between the behaviours given and received it is not possible to establish if grooming was used to appease current aggressors' renewed aggression or/ and to service a partnership which might buffer against future potential aggressions

from the groomee. Neither can we determine if the aggressors' aggressive behaviours were actually instances of side-directed or redirected aggression against partners they were bonded to.

12. The test of the covariation hypothesis confirmed that the rates of counter-aggression and post-conflict affiliation, and the initiation of post-conflict affiliation by aggressors were intercorrelated and were associated with the more egalitarian dominance style of the gelada group.

13. The study provided support for the prediction of the relational model that the rates of affiliative behaviour were observed to increase markedly soon after the aggressive conflicts had ended. In other words, there was the predicted quick switch in the antagonists' motivation, from aggression to affiliation.

14. Although the methods of study adopted in this research, that is, correlational (at group level), cross-sectional, and comparative with just one group per species, were comparable to those that are considered standard in this field, however, it is fair to acknowledge that some of the conclusions drawn from this study can only be regarded as tentative, even if they are supported by previous work. The small size of one of the groups, the lack of (short-term) contingency data, and the lack of matched-control observations of conflicts were the most important limitations of this study.

15. The findings from this study add to the growing contemporary perspective on the bonded nature of primate sociality, where individuals are regarded as 'traders' that actively budget their social time to service their welfare- and fitness-enhancing bonds and cooperative partnerships. They show that individuals compete and cooperate through the reciprocal or unidirectional exchange of services (grooming and support) and the repairing of bonds disrupted by aggression through post-conflict friendly exchanges. The study also highlights the importance of demographic constraints that lead to fast changes in the biological market (e.g., dominance gradients) and of phylogenetic constraints that cause the evolution of correlated traits (e.g., dominance styles). Finally, this research is a contribution to the notion that the strategies of social behaviour seen in social groups reflect the operation of processes of partner choice, where individuals engage in outbidding competition and switch partnerships when the cost/benefit ratio is no longer balanced.

# RESUMEN

La *socialidad* o *vida en grupo* ha evolucionado independientemente en muchas especies de animales, pero sólo en algunas de ellas se sustenta en *vínculos sociales* entre los miembros del grupo, que son gestionados a través del intercambio de diversos comportamientos sociales con múltiples compañeros. Esta *socialidad basada en vínculos* de los primates no humanos (y de los humanos) y de algunas otras pocas especies se caracteriza por apoyarse en la *prosocialidad* o *cooperación* entre individuos que normalmente se conocen bien entre ellos y que se involucran en asociaciones duraderas y altamente individualizadas. Los patrones de socialidad y prosocialidad observados en los primates reflejan los 'trade-offs' (compromisos) entre varias actividades antagónicas que aumentan el bienestar y la eficacia biológica y, en última instancia, son el resultado de la manera en que los individuos gestionan eficazmente sus inevitables *conflictos de intereses* a través de estrategias de *competencia agresiva*, de *cooperación* y de *reconciliación post-conflicto*. La teoría contemporánea sobre la socialidad y la prosocialidad de los primates coloca el acento en la necesidad de integrar la *socio-ecología* (es decir, factores ecológicos, demográficos y sociales), la *filogenia* (historia evolutiva) y la *historia vital* (rasgos de historia vital) en cualquier descripción de las *causas inmediatas y* últimas de la variación en los sistemas sociales de los primates.

La presente investigación pretende estudiar la socialidad y prosocialidad en dos grupos de babuinos africanos, el gelada (*Theropithecus gelada*) o babuino de montaña y el mandril (*Mandrillus sphinx*) o babuino de bosque, ubicados en cautividad en espacios naturalizados, amplios y con vegetación. La orientación del estudio ha sido teórica en cuanto a que se ha dirigido a probar varias hipótesis y predicciones específicas, las cuales se describen de forma exhaustiva en los tres capítulos empíricos de la tesis (capítulos 2-4). El enfoque metodológico adoptado fue observacional y comparativo. Los objetivos generales de esta investigación pueden formularse como se indica a continuación:

1. Analizar los presupuestos de tiempo de actividad de dos especies diferentes en condiciones ecológicas igualmente benignas, es decir, alimentados y libres de depredación, y probar dos modelos alternativos con respecto a las categorías de

presupuestos de actividad que cabría esperar que aumentaran (o disminuyeran) cuando a los individuos se les libera de estrés ecológico (capítulo 2).

2. Llevar a cabo un estudio más fino sobre el comportamiento socio-espacial de las dos especies evaluado a través de dos índices, el de socialidad (tiempo acompañados *versus* solos) y el de gregarismo (número de 'vecinos' cuando están acompañados) en cuatro categorías diferentes de distancia social (capítulo 2).

3. Probar la predicción de la teoría del mercado biológico que defiende que la variación en el gradiente de dominancia del grupo influirá en los patrones de reciprocidad e intercambio de acicalamiento y de comportamiento prosocial (es decir, castigo altruista) (capítulo 3).

4. Probar la predicción de la hipótesis de covariación que establece que los patrones de manejo de conflictos tienden a intercorrelacionar y están relacionados con el estilo de dominancia y el grado de asimetría ('steepness') de la jerarquía del grupo (capítulo 4).

5. Poner a prueba la predicción del modelo Relacional que indica que los individuos que han participado en un encuentro agonístico es probable que experimenten un cambio rápido de un modo o tono de motivación agresivo a otro de carácter amistoso nada más terminar el conflicto (capítulo 4).

El estudio se realizó desde octubre de 2010 hasta abril de 2011 en La Vallée de Singes, un parque de elevada superficie de simios y antropoides situado en Romagne (Francia). Los sujetos eran los miembros de un grupo de 9 geladas, *Theropithecus gelada* y de un grupo de 17 mandriles, *Mandrillus sphinx.* Los recintos eran de elevadas dimensiones (2,800 y 3,500 m2), con vegetación y completamente equipados con una variedad de dispositivos de enriquecimiento. El estudio consistió en el muestreo y registro de (a) cuatro categorías generales de *actividad conductual*, es decir, *en movimiento*, *forrajeo/alimentación*, *descanso* y *socialización*; la categoría de actividad social se desglosó en tres subcategorías, a saber, *afiliación*, *agresión* y *juego social*; (b) cuatro categorías de *distancia social*: *en contacto, dentro del alcance de un brazo*, *entre uno y dos brazos de alcance* y *entre dos brazos y 4 metros*; y (c) un gran repertorio de comportamientos *asertivos* [suplantar, presentar], *agonísticos* (agresivos [por ejemplo, amenazar, golpear] y sumisos [p. ej., *exposición de dientes*, *huir*]), *afiliativos* [por ejemplo, acicalamiento] y *cooperativos* [por ejemplo, apoyar y castigar a agresores o víctimas]. Estos registros conductuales fueron muestreados mediante técnicas de muestreo de *focal-individual* y *focal-grupal* y fueron recogidos a través de *muestreos instantáneos* y de *registro continuo* durante un periodo de 22 semanas. Los datos brutos se transformaron en diferentes medidas conductuales que fueron utilizadas para analizar las preguntas específicas planteadas en los tres capítulos empíricos. Se utilizaron los registros de actividades conductuales y conductas socio-espaciales para estudiar los *presupuestos de tiempo de actividad* y *socialidad* y *gregarismo* (capítulo 2), y los registros sobre las conductas agonísticas, amistosas y cooperativas fueron utilizados para estudiar los *grados de dominancia* y *la reciprocidad y el intercambio* de *agresión*, de *acicalamiento* y de *castigo* (capítulo 3) y para estudiar los *estilos de dominancia* y las *estrategias* de *gestión* de *conflictos* (capítulo 4).

Los principales resultados y conclusiones de este estudio se resumen a continuación:

1. A pesar de vivir en un entorno ecológico libre de depredadores y con provisión de alimento, los presupuestos de actividad de los dos grupos de estudio cayeron dentro del rango de variación de los *presupuestos de la actividad* que se han descrito para las poblaciones en libertad de geladas y babuinos *Papio* que están ecológicamente estresados. Este hallazgo plantea la interrogante sobre por qué en condiciones ecológicas tan benévolas a las que los dos grupos se enfrentaron en cautividad, las decisiones sobre el presupuesto de tiempo actividad de los individuos fueron tan resilientes.

2. Aunque los presupuestos de actividad de los dos grupos resultaron similares, no fueron idénticos. Los geladas y los mandriles dedicaron altos niveles de su presupuesto de tiempo al forrajeo, sin embargo, los primeros tuvieron niveles más altos de actividad *social* que de *movimiento,* mientras que los segundos dedicaron más tiempo al *descanso,* que a la *actividad social*.

3. En ambos grupos, el tiempo dedicado al *comportamiento amistoso* fue mucho mayor que el invertido en *agresión*. Este patrón también se ha registrado en poblaciones salvajes. Los resultados obtenidos corroboran la afirmación de que la relación entre la cautividad y el comportamiento está lejos de ser sencilla. Dentro de ciertos límites de variación ecológica y en especies con una enorme evolución social muy sofisticada, los individuos parecen ser más sensibles a las características sociales y demográficas de los nichos socio-ecológicos presentes en condiciones de cautividad que a otras variables asociadas típicamente con escenarios de cautividad.

4. Se ha observado que los individuos de los dos grupos de estudio estuvieron la mayor parte del tiempo sólos, es decir, sin vecinos, dentro de un radio de alcance de dos brazos. Esta débil *socialidad* fue compartida por ambas especies; no obstante, los geladas puntuaron más que los mandriles en *socialidad* en todas las categorías de distancia social analizadas.

5. En ambos grupos, el *gregarismo* de los individuos, es decir, el número de vecinos encontrados en las distintas categorías de distancia social, resultó ser más bien reducido. Cuando estuvieron acompañados en un radio de dos brazos de distancia, apenas hubo más de dos individuos. Y en la distancia más lejana este patrón no fue tampoco muy diferente. Al igual que con la socialidad, los geladas fueron también más gregarios que los mandriles. Esta organización socio-espacial basada en la formación de grupos de dos (dúos) o de tres (tríos) resulta intrigante y plantea cuestiones importantes con respecto a la naturaleza de la cohesión del grupo y sus bases conductuales, psicológicas y socio-ecológicos.

6. La jerarquía de dominancia del grupo de mandriles fue más asimétrica que la de los geladas. Contrariamente a las predicciones de la teoría del mercado biológico, el acicalamiento fue intercambiado recíprocamente, con independencia de la variación en el gradiente de dominancia. En línea con las expectativas, hubo un intercambio negativo (unidireccional) de acicalamiento por castigo en el grupo con mayor gradiente de dominancia; sin embargo, esta correlación sólo fue marginalmente significativa.

7. El rango de dominancia resultó ser un buen predictor de la distribución de los comportamientos de agresión diádica y triádica; sin embargo, no predijo la distribución de medidas amistosas (acicalamiento). Esta independencia del acicalamiento respecto al rango podría explicar por qué fue recíprocamente correspondido en lugar de intercambiado por apoyo agonístico o, en nuestro estudio, la evitación de castigo.

8. Se encontró una relación estrecha entre el acicalamiento y el tiempo pasado en asociación espacial (es decir, asociaciones de proximidad). Sin embargo, en varios casos, los patrones de reciprocidad e intercambio encontrados fueron independientes de las relaciones de proximidad. Es decir, los individuos mostraron relativamente más a menudo una conducta dada a aquellos de quienes recibían relativamente más a menudo esa misma conducta (en reciprocidad) u otra conducta (en intercambio) a cambio. Esto significa que la reciprocidad o el intercambio eran genuinos y no producto de la proximidad.

9. Como se esperaba, la agresión y el castigo a la víctima, donde las diferencias de poder entre los castigadores y las víctimas eran más elevadas, fueron ambos unidireccionales, un patrón que era más fuerte en el grupo con una jerarquía de dominancia más asimétrica. Y, como se esperaba, el castigo al agresor fue recíproco en el grupo con menor gradiente de dominancia.

10. Las intervenciones agresivas por parte de terceros fueron generalmente dirigidas hacia abajo en la jerarquía, lo que implica que se tendían a minimizar los riesgos de represalias. Sin embargo, en el grupo más igualitario de geladas, algunas de las intervenciones no fueron ‘conservadoras’, sino ‘puente’, lo cual significa que los interventores apoyaban al individuo de menor rango (es decir, la víctima) contra el oponente de rango medio (es decir, el agresor).

11. La agresión fue intercambiada por acicalamiento. Dado que el estudio no analizó las contingencias a corto plazo entre los comportamientos dados y recibidos no es posible establecer si el acicalamiento fue utilizado para apaciguar una nueva agresión del agresor y/o amortiguar futuras agresiones potenciales del espulgado. Tampoco podemos determinar si los comportamientos agresivos de los agresores fueron en realidad casos de agresiones dirigidas o redirigidas contra compañeros a los que estaban vinculados.

12. La prueba de la hipótesis de covariación confirmó que las tasas de contra-agresión y de afiliación post-conflicto, y la iniciación de afiliación post-conflicto por los agresores estuvieron intercorrelacionadas y estaban más asociadas con el estilo de dominación más igualitario del grupo de geladas.

13. El estudio sustanció empíricamente la predicción del modelo relacional que sostiene que los índices de comportamiento amistoso deberían elevarse notablemente poco después de que concluya un conflicto agresivo. En otras palabras, se observó el cambio rápido previsto por el modelo Relacional en la motivación de los antagonistas, de agresiva a amistosa.

14. Aunque los métodos de estudio adoptados en esta investigación, es decir, el correlacional (a nivel de grupo), y el transversal y comparativo con un solo grupo por especie, fueron comparables a los que se consideran estándar en este campo, cabe reconocer que algunas de las conclusiones de este estudio sólo deben considerarse provisionales, aun cuando éstas sean coincidentes con las alcanzadas en trabajos

anteriores. El reducido tamaño de uno de los grupos, la falta de datos sobre contingencia (a corto plazo) y la falta de observaciones control sobre los conflictos, han sido las limitaciones más importantes de este estudio.

15. Los resultados de este estudio apoyan la perspectiva contemporánea sobre la naturaleza de la socialidad basada en vínculos de los primates, donde los individuos son considerados como 'comerciantes' que gestionan activamente su presupuesto de tiempo social al servicio de vínculos sociales que mejoran su bienestar y su salud y la calidad de sus relaciones cooperativas. Se demuestra que los individuos compiten y cooperan mediante el intercambio recíproco o unidireccional de servicios (acicalamiento y apoyo) y la reparación de vínculos rotos por agresiones a través de intercambios amistosos post-conflicto. El estudio también destaca la importancia de las restricciones demográficas que conducen a cambios rápidos en el mercado biológico (como los gradientes de dominancia) y de las restricciones filogenéticas que causan la evolución de rasgos correlacionados (por ejemplo, los estilos de dominancia). Finalmente, esta investigación es una contribución a la noción de que las estrategias de comportamiento social en los grupos sociales reflejan la operación de procesos de elección de 'socio', donde los individuos participan en una competición de puja y cambian de socio cuando la relación coste/beneficio no resulta suficientemente equilibrada y rentable.

# CHAPTER 1

# General Introduction and Objectives

## Defining social systems and its components

There has been a long debate and a variety of typically complementary proposals to define the components that need to be addressed in the study of social systems (see Kappeler and van Schaik, 2002, Kappeler *et al.,* 2013; Nystrom & Ashmore, 2008; Fuentes, 2011; Schülke & Ostner, 2012; Koenig *et al.* 2013, for recent reviews). For example, Kappeler and van Schaik (2002) proposed three components: social organization, mating system, and social structure. *Social organization* is defined in terms of the "size, sexual composition, and spatiotemporal cohesion of a society" (p. 710). This component is a bit heterogeneous, though, as, in addition to grouping patterns (e.g., group cohesion and stability), it conflates two different dimensions of demography that would be worth keeping apart (Dunbar, 1988), that is, demographic structure (e.g., group size, operational sex ratio, group relatedness among group members) and demographic processes (e.g., birth and death rates and dispersal patterns). Colmenares (2015) has thus proposed a scheme of four components (Fig. 1.1): grouping patterns and demographic structure, demographic processes and dispersal patterns, mating and parenting systems, and group structure. Before we provide a brief overview of the main theoretical frameworks that have been proposed to account for the patterns of variation observed in these four components of a social system we will define briefly what variables are traditionally analysed in each of them.

### *Component 1: Grouping patterns and demographic structure*

The diversity of primate grouping patterns is typically classified into a variable number of categories and subcategories. Kappeler and van Schaik (2002) distinguished three major categories: solitary, pair-living and group-living. However, within these categories, finer subcategories can yet be identified. For example, the group-living, bisexual group

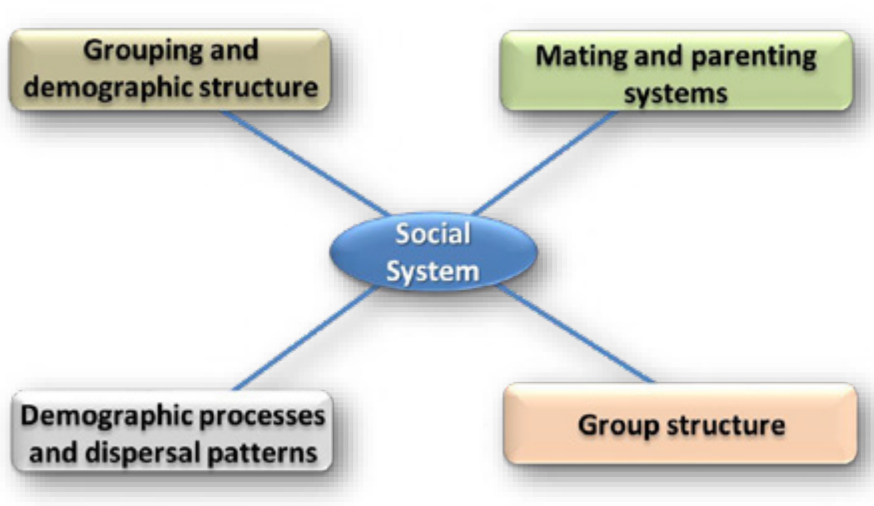

**Figure 1.1** The four components of social systems (after Colmenares, 2015).

category, which is the most frequent type of social organization found among primates, can come in several versions, namely, the single-male/multi-female group, the single-female/multi-male group and the multi-male/multi-female group (e.g., Nystrom and Ashmore, 2008). And the multi-male/multi-female groups can be further variously organized into multi-level (e.g., the hamadryas baboon, *Papio hamadryas*, Abegglen, 1976, Kummer 1984, Schreier and Swedell, 2009; and the gelada baboon, *Theropithecus gelada*, Kawai *et al*., 1983, Dunbar, 1988; see Colmenares, 2004, for a review), and fusion-fission (Aureli *et al.,* 2008). Recently, the multi-level type of social grouping has also been labelled modular or nested (Grueter, Chapais and Zinner, 2012; Schreier and Swedell, 2012).

It is worth mentioning that some authors have used this component of social systems, i.e., social organization, with a different meaning. In fact, they have defined 'social organization' in the same terms as 'social structure' and *vice versa* (see below, *component 4*, social structure). Thus, Rowell (1979) defined social organization in terms of the "patterns of social interaction among individuals", whereas social structure was defined in terms of "population density, group size, and demographic character" (p. 5). Rowell has actually used these two labels, social structure and social organization, in different ways, for example, in 1971 she stated that "…*social structure* [can be] built up by asking the basic question 'who did what to whom how often'…" (Rowell, 1971, p. 625; my italics), but some years later she wrote "The *social organization* of monkey groups has been generally described in terms of 'who does what to whom how often'…" (Rowell and Olson, 1983; my italics). Bernstein has also used the label 'social organization' with the same meaning as in Rowell's (1979) original definition (e.g., Bernstein and Williams, 1986).

*Component 2: Demographic processes and dispersal patterns*

The variables that capture the demographic processes typically occurring in populations and groups of primates (and other species) are birth rate, death rate, and dispersal (i.e., male-biased, female-biased or dispersal by either sex) into and out from the natal group upon reaching sexual maturity or across groups during adulthood (Pusey and Packer, 1987). Needless to say that these *dynamic* processes determine at any given point of time the demographic (*static*) structure of a group, that is, its size, its operational sex ratio, the sex ratio of different age-sex classes and the group's kinship structure (Dunbar, 1988).

*Component 3: Mating and parenting/rearing patterns*

The mating systems are defined in terms of the number of individuals of each sex that are actually actively contributing to the group's breeding (which typically differs from the number of sexually mature individuals of each sex residing in the group, especially in species with harem-defence polygyny), whether individuals mate with one or multiple members of the other sex, as well as the stability of mating partnerships (Clutton-Brock, 1989; Davies, 1991; Davies, Krebs and West, 2012). They are classified into the following categories: *monogamy* (which can be obligate or facultative, long-term or serial); *polygyny*, i.e., one male with multiple females (which can be further divided into several subcategories such as, for example, female or harem defence polygyny or territory defence polygyny); *polyandry*, i.e., one female with multiple males; *polygynandry*, i.e., both sexes are polygamous; and *promiscuity*, i.e., both sexes are polygamous and mating partnerships or bonds tend to be short-lived. The majority of these mating systems can be found in primates (Dunbar, 1988; Kappeler and van Schaik, 2002; Nystrom and Ashmore, 2008; Fuentes, 2011).

As members of the Class *Mammalia* (Clutton-Brock, 1991; Eisenberg, 1981; Vaughan, Ryan and Czaplewski, 2011), all primate mothers are heavily and mostly solely involved in parenting (i.e., uniparental care) of the relatively few infants (typically as singletons) they produce throughout their lifetimes (Martin, 1980; Emery Thompson, 2012), except in those species that are monogamous and then males share some of the burdens of caring for their offspring (Snowdon, 1996; Muller and Emery Thompson, 2012). In many cases, especially in species with male dispersal, mothers establish lifelong bonds with their daughters; this means that they can provide continued long-term investment (for example, help in fights) in their daughters' welfare until they die (van Noordijk, 2012).

### *Component 4: Group Structure*

This is defined in terms of the content, quality and temporal patterning of *social relationships* between all the dyads of individuals in the group which, in turn, are defined in terms of the content, quality and temporal (e.g., contingent) patterning of the observable behaviours used by the group's members in their *social interactions* with one another (Hinde, 1976). This conceptual scheme has been very influential in this research area (Hinde, 1983; Dunbar, 1984, 1988; Kappeler and van Schaik, 2002; Brent, Lehmann and Ramos-Fernández, 2011; Whitehead, 1997, 2008). Of course, the conceptualization of social relationships and social interactions has been greatly refined over the years in various ways. For example, de Waal (1986, 1987) emphasized the importance of taking into account triadic (and polyadic), not just dyadic, interactions as well as the social context in which individuals interact with one another (see also Kummer, 1975; Mason, 1978; Vaitl, 1978; Colmenares and Rivero, 1986) and Cords and Aureli (2000) and Silk, Cheney and Seyfarth (2013) elaborated the categorization of relationship components and properties that can be used to gain a sharper understanding of social relationships (value, compatibility and security *versus* frequency, diversity, symmetry, tenor, tension, predictability and stability, respectively).

As noted above, some early authors defined social structure in the terms that most contemporary researchers have adopted to define social organization and *vice versa* (see Whitehead, 2008, p. 8), and some researchers have used both categories interchangeably (Whitehead, 1997, p.1053). In the present study we will stick to the contemporary concept of social structure that has gained the greatest consensus.

## Accounting for variation in primate social systems

The three main theoretical frameworks that have been used to account for the observed patterns of variation both between species and within species in primate social systems are the socio-ecological theory, phylogeny or evolutionary constraints, and the life-history theory (see Chapman and Rothman, 2009; Clutton-Brock and Janson, 2012; Di Fiore and Rendall, 1994; Fuentes, 2011; Kappeler *et al.,* 2013; Koenig *et al.,* 2013; Kutsukake, 2009; Parga and Overdorff, 2011; Schradin, 2013; Schülke and Ostner, 2012; Shultz, Opie and Atkinson, 2011; Thierry, 2008, 2013; van Schaik, 2016, van Schaik and Isler, 2012, for recent reviews). Of course, socio-ecological factors and phylogenetical and life history constraints are all regarded as intertwined, jointly shaping the behavioural responses of individuals, their social relationships and, ultimately, their groups' social structures. They are now briefly sketched.

### *Socioecological theory*

It focuses on the assessment of the impact of ecological factors, including predatory risk, abundance and distribution of food, and risk of conspecific aggression and infanticide, on grouping patterns, demographic processes, and the ecological and social behaviour of individuals (e.g., foraging strategies, social strategies of competition and cooperation). There are multiple feedback loops involved that can operate at various levels. For example, predation risk and food monopolizability will favour the formation of larger groups of females and males (multi-male/multi-female groups); this will lead to higher levels of intra-group contest competition, which will favour mating promiscuity, paternity uncertainty, female philopatry, and despotic (strict) dominance relationships and nepotistic (kin-biased) bonds and alliances among females (e.g., Isbell, 1991, 1994; van Schaik, 1989; Sterck, Watts and van Schaik, 1997; Wrangham, 1980).

### *Phylogeny and evolutionary history*

A key variable that was overlooked in early formalizations of socioecological theory is phylogeny. Evolutionary history and intercorrelated evolution have been shown to greatly constrain the range of plasticity and flexibility of groups' and individuals' behavioural responses to current and typically fluctuating local ecological and demographic conditions (Di Fiore and Rendall, 1994; Thierry, 2008, 2013; Chapman and Rothman, 2009; Shultz *et al*., 2011; Balasubramaniam *et al.,* 2012; Koening *et al.,* 2013). For example, Di Fiore and Rendall (1994) found that the social systems of primates, especially of Old World monkeys, are strongly conserved (these authors used the labels social system and social organization as synonymous, actually with the contemporary meaning of social structure). What is most remarkable and indeed interesting is that this salient social system uniformity among cercopithecoids occurs despite the fact that they are the most ecologically diverse primate taxa (inhabiting the most extensive variety of habitat types) that have driven the evolution of all sorts of anatomical and physiological adaptive specializations that enable them to effectively exploit the bewildering diversity of substrates and diets they encounter and copy with.

### *Life history theory*

The basic tenet of life history theory is that a species' set of life history traits or parameters (e.g., age at weaning, age at first reproduction, life expectancy at birth and at sexual maturity, birth rates and longevity) reflects the evolutionary outcome of the optimization of a number of trade-offs between allocation targets that are antagonistic, that is, that present a negative functional interaction between them (Stearns, 1989). This means that increased allocation to any one target reduces the individual's ability to allocate time or energy to others (for example, growth and maintenance *versus* reproduction; current *versus* future reproduction; mating *versus* parenting effort). Primates are a characteristically slow-developing mammalian Order (Martin, 1990), so they exhibit the whole set of characteristic slow-paced life history traits, including low extrinsic mortality and long life expectancy. This condition has consequences on a plethora of phenotypic traits, including their behavioural plasticity, their brain size, and their cognitive skills (van Schaik, 2016; van Schaik and Isler, 2012). In the behavioural domain, for example, the slow-paced life history syndrome has selected for individuals that are risk averse in the face of threat of predation or conspecific aggression. This evolved risk aversion has in turn selected for sociality or group living, that reduces predatory risk, and for prosociality or cooperation, that buffers against increased sexual coercion and infanticide risk and against increased intra-group aggressive competition for resources.

## The study of group structure

The study of group structure requires attention be paid to at least four dimensions of social behaviour (Colmenares, 2015): aggression, affiliation, reconciliation and cooperation (Fig. 1.2). All of these dimensions will be addressed in the research reported here.

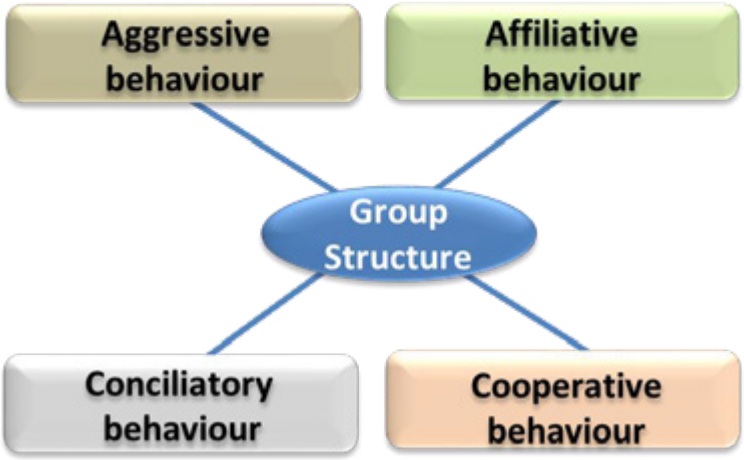

**Figure 1.2** The four components of social systems (after Colmenares, 2015).

### *Social time and time budgets*

Primates spend their daytime engaged in four time-consuming, biologically relevant and mutually incompatible activities, namely, moving, resting, foraging, and socializing (this includes affiliative and aggressive behaviours and social play). Evolutionary theory claims that natural selection should be expected to shape the individuals' time budget allocation decisions so as to maximize their fitness, that is, they should flexibly adjust them to current local conditions. One of the key and rather controversial issues tackled in this area has been to understand how individuals adjust their time budgets under conditions that vary in the levels of ecological (food) stress and, therefore, in the time allocated to foraging (Dunbar, 1992b; Bronikowski and Altmann, 1996).

### *Socio-spatial behaviour*

Primate individuals are known to form non-random, temporally stable spatial associations with a subset of their group mates (Bret *et al.,* 2013; Pasquaretta *et al.,* 2014). However, the study of animal ‘proxemics’ has received very little attention. It is remarkably unclear, for example, how much time individuals spend at various social distance categories of others and with how many neighbours they associate at those different distances. This information, if available, could provide us with very relevant clues about the actual socio-spatial mechanisms that sustain any grouping pattern and more generally a group’s cohesion, in terms of closeness (intimacy), sociality (as opposed to solitariness), and gregariousness (number of neighbours).

### *Agonistic, affiliative and cooperative behaviour*

Primate sociality is typically bonded and bonds need to be serviced if they are to enhance the individuals’ welfare and fitness (Dunbar and Shultz, 2010; Kummer, 1978; Seyfarth and Cheney, 2012; Silk, 2012). The partnerships that sustain a group’s bonded sociality are thought to be the outcome of the incumbent individuals’ aggressive, affiliative, and cooperative strategies (Kummer, 1978; Dunbar, 1988; Cords, 1997). Some researchers have argued that affiliative behaviours such as grooming and cooperative behaviours such as help in fights can be regarded as ‘services’ or ‘commodities’ that individuals reciprocate for themselves or interchange for others (de Waal and Luttrell, 1988; de Waal and Brosnan, 2006; Hemelrijk, 1990a, 1990b; Hemelrijk and Puga-Gonzalez, 2012; Schino and Aureli, 2008a, 2008b, 2009; Seyfarth and Cheney, 1988). For years, the standard theoretical model to account for the evolution of cooperation between unrelated individuals was Trivers’ (1971, 2006) theory of reciprocal altruism. This places emphasis on reciprocity (or lack of it) between individuals that interact with each other repeatedly (i.e., the iterated prisoner’s dilemma) as the crucial mechanism that controls for altruism and against defection (i.e., the so-called ‘partner control model’). This view has been challenged by the so-called Biological Market Theory (BMT) that provides an alternative account for the evolution of cooperating partnerships and the underlying mechanism that protects against defection, namely, partner choice (Noë and Hammerstein, 1994, 1995; Hammerstein and Noë, 2016; Schino and Aureli, 2016). One of the predictions of the BMT is that the value of any one service (e.g., grooming or agonistic support) is not fixed, but variable, and what its value depends on the law of supply and demand. In this regard, it has been argued that the value of agonistic support increases as the group’s dominance hierarchy gets steeper, and the prediction has been made that when a group’s dominance gradient is high, low-ranking individuals should be expected to trade grooming for agonistic support from high-rankers rather than to engage in reciprocal grooming (Barrett, 2001, 2006). So far, the tests of this prediction have yielded mixed results (e.g., Kaburu and Newton-Fisher, 2015).

### *Conflict-management strategies*

Sociality does inevitably lead to conflicts of interest between group members and since some of these conflicts are likely to escalate to serious fights, social species should be expected to have evolved adaptations to mitigate the potentially dispersive consequences (as well as other negative side-effects) of aggressive escalation (de Waal and Roosmalen, 1979, de Waal, 1993, 2000a, 2000b). This has come to be called the *theory of reconciliation*; it claims that in social species, antagonists are more likely to make friendly contacts after conflicts than in control conditions without aggression.

de Waal challenged the classical view about the causes, the process, and the consequences of social aggression, the so-called *individual model of aggression*, put forward by early ethologists (e.g., Lorenz, 1965) and dominant in the field and in popular wisdom for decades. According to this model, the individuals that have been involved in an aggressive encounter, i.e., the antagonists, will tend to move away from one another (i.e., spacing is increased), will exhibit negative emotions towards one another (i.e., their post-conflict emotions and motivations will be continuous with aggression), and will face a disruption of social bonding (i.e., their dyadic relations and the group's cohesion will be jeopardized). de Waal (1993, 2000b) came up with an alternative view, the so-called *relational model of aggression*, that challenged and overturned the classical model and its three major premises. He claimed that in socially-living species, individuals crucially depend on their bonds with one another and, therefore, it is these social bonds themselves that become resources as vital for their fitness as food, water, and so on are. So, individuals would be expected to invest time and energy to service, protect, preserve and repair these bonds from any disruption that can jeopardize them, especially in the face of within-group aggressive conflicts. According to the relational model, in social species tolerance (increased threshold for initiating aggression) and avoidance (increased tendency for avoiding aggressive escalation) would be important components of the individuals' evolved psychology. Nevertheless, even in the best of the possible scenarios aggression will never be completely suppressed; however, when individuals do get involved in an aggressive encounter, they can use a number of post-conflict strategies to manage the effects of aggression and restore pre-conflict levels of affiliation in their mutually valued social relationship. The relational model also claims that following aggression, individuals will exhibit a discontinuous motivation, that is, they will quickly switch from hostility to affiliation, they will so suppress the tendency to space out after aggression, and finally, they will restore their bonds temporarily disrupted by the aggressive confrontation. Although the original impetus for the study of conflict-resolution strategies focused on primates (see Aureli and de Waal, 2000; Aureli, Cords, and van Schaik, 2002; Arnold and Aureli, 2007; Arnold, Fraser and Aureli, 2011; Aureli *et al.,* 2012; Colmenares, 1996b, 2006 for reviews), tests of the reconciliation hypothesis and the relational model have also been done with a handful of non-primate mammals (dolphins: Yamamoto *et al.,* 2016; elephants: Plotnik and de Waal, 2014; hyenas: Wahaj, Guse, and Holekamp, 2001; dogs: Riemer et al., 2013; Cools, van Hout, and Nelissen, 2008; wolves: Cordoni and Palagi, 2008; Palagi and Cordoni, 2010; Baan et al., 2014; goats: Schino, 1998) and even birds (rooks: Seed, Clayton, and Emery, 2007; Logan, Ostojic and Clayton, 2013; ravens: Fraser and Bugnyar, 2011), with similarly positive results.

A crucial dimension of a group's social structure is dominance, broadly defined as the ability to monopolize resources in competitive contexts. And groups (and species) can be classified in terms of its predominant so-called *dominance style* (de Waal, 1989a, 1989b; de Waal and Luttrell, 1989; Flack and de Waal, 2004; Matsumura, 1999), which is typically defined in terms of the frequency, severity and direction of aggressive exchanges, the dominance gradient, the presence of unidirectional and formal status signals of dominance/subordinance, the social tolerance around resources (food, water, attractive partners), and the patterns of conflict resolution (e.g., conciliatory tendency; initiation of conciliatory approaches; types of conciliatory behaviours; presence of consolation and third-party affiliation). To account for the patterns of variation in their *social styles*, Thierry (2000, 2004) formulated the *Covariation Hypothesis* which claims that variation in many behavioural traits is actually correlated and that phylogeny may have a greater impact than ecology. So far, most tests of this hypothesis have been done on *Macaca* and have generally confirmed its predictions (Thierry, 2007, 2008, 2013; Thierry *et al.,* 2008; Berman and Thierry, 2010).

## Methodological approaches to studying sociality and prosociality

Sociality and prosociality, like any other behavioural process, can be studied observationally or experimentally, longitudinally or cross-sectionally. These methodological approaches are all scientifically sound and typically yield complementary and mutually fertile information. Of course, all of them have strengths and weaknesses, but its utility is more related to the question that has been asked than to anything else (Altmann, 1974; Dunbar, 1976; Lehner, 1996; Martin and Bateson, 2007; Stamp Dawkins, 2007).

Comparisons are inevitable in scientific endeavours, as they are required for identifying both patterns of covariation in observational/correlational studies as well as causal relations between independent and dependent variables in experimental studies. However, the comparative approach takes on an additional flavour in biology and in behavioural biology and comparative psychology as it typically refers to comparisons across species. Timberlake (1993) classified the types of comparisons that are made in animal behaviour (i.e., ethology and comparative psychology) into four categories on the basis of crossing two dimensions, genetic affinity *versus* ecological affinity. This led to his 2 x 2 table of methods of comparing behaviour: protoevolutionary (low both genetic and ecological affinities), ecological (low genetic affinity and high ecological affinity), phylogenetic (high genetic affinity and low ecological affinity), and microevolutionary (high both genetic and ecological affinities). Comparative studies have become highly sophisticated with the advent of powerful phylogenetical statistical techniques that control for phylogenetic relatedness. In the field of animal behaviour, these techniques have been widely used in studies of behavioural and cognitive evolution (e.g., social systems: Di Fiore and Rendall, 1994; social behaviour; Thierry *et al.*, 2000; prosociality and hyper-cooperation: Burkart *et al.,* 2014; cognition: MacLean *et al.,* 2012).

### Geladas (*Theropithecus gelada*) and Mandrills (*Mandrillus sphinx*) compared

The tribe *Papionini* comprises several genera (Grubb *et al.,* 2003), some living in Africa, i.e., African papionins (baboons, mandrills, and mangabeys), and others living in Asia, i.e., Asian papionins (macaques) (Jolly, 2007). Papionins belong to the subfamily *Cercopithecinae* (cheek-pouched primates), family *Cercopithecidae*, superfamily *Cercopithecoidea* (Groves *et al.,* 2003).The species studied in the present research are the gelada, *Theropithecus gelada*, Rüppell 1835, and the mandrill, *Mandrillus sphinx*, Linnaeus 1758. They are referred to as montane baboons and forest baboons, respectively (Stammbach, 1987), as those are the habitats where they are typically found, that is, montane grasslands ranging in altitude from 2100 to 3900 m (Dunbar, 1992a), and primary and secondary dense rain forests, gallery forests and forest-savanna mosaics (Harrison, 1988), respectively. Although mandrills are rather similar to geladas and the *Papio* baboons in their social organization and group structure, however, they are phylogenetically closer to mangabeys (genus *Cercocebus*), as evidenced by the host of morphological and dental features they share with them (Fleagle and McGraw, 2002).

Geladas and mandrills are said to differ on a number of traits (see Swedell, 2011 for a review), including their mating system, i.e., polygynous *versus* polygynandrous, respectively; and their overall social system, i.e., multilevel-modular/nested *versus* multimale-nonmodular, respectively (Colmenares, 2004; Grueter and Zinner, 2011; Snyder-Mackler, Beehner, and Bergman, 2012; Tinsley Johnson *et al.*, 2014). In geladas, female dominance relationships and hierarchies within one-male units (OMUs) are highly differentiated, and female-female bonding, as expressed in grooming and aiding behaviours, is strongly kin-biased (Dunbar, 1984; Le Roux *et al.,* 2011; Tinsley Johnson *et al.,* 2014). Unfortunately, comparable data on wild mandrills are lacking, although the species is also classified as female-bonded and female philopatric (Swedell, 2011). In this species, male-male intra-sexual competition is intense as evidenced by the extreme sexually dimorphic ornaments, body size, and weaponry deployed by males and the well-developed agonistic dominance relationships they form (Dixon, Bossi, and Wickings, 1993; Grueter *et al.,* 2015; Setchell and Wickings, 2005). In contrast, we know near to nothing on male-female relationships, and on female bonding and dominance relationships in this species. Setchell, Knapp, and Wickings (2006) reported on an instance of a female-female coalition against a male, suggesting that, like in geladas, male-female dominance relationships in mandrills may not be as asymmetric as they are in other closely related species of papionins (i.e., hamadryas baboons, Colmenares, 2004; Kummer, 1995; Stammbach, 1987). Also, we do know that mandrill groups form dominance relationships in captivity (Emory, 1976; Feistner, 1989; Holt, 1980). Unfortunately, neither geladas' nor mandrills' social styles have been clearly chartered; even though the former's social system has been thoroughly described in the wild (e.g., Dunbar, 1984, 1992; Kawai *et al.,* 1983; Snyder-Mackler *et al.,* 2012).

## Objectives

The present research was aimed to study sociality and prosociality in two groups of African papionins, geladas (*Theropithecus gelada*) and mandrills (*Mandrillus sphinx*), housed in rather similarly naturalized, sized and vegetated enclosures in captivity. The study was largely theory-driven and was aimed to test several specific assumptions and predictions. These are fully spelled out in the chapters 2 through 4. Nevertheless, the general objectives of this research can be stated as follows:

1. To analyse the activity time budgets of two different species housed in similarly benign ecological conditions, that is, food-provisioned and predation free, and test two competing models regarding the activity budget category that should be expected to increase (or decrease) when individuals are freed of ecological stress.

2. To carry out a fine-grained study of socio-spatial behaviour of the two species in terms of sociality (time spent accompanied *versus* alone) and gregariousness (number of neighbours when accompanied) at four different social distance categories.

3. To test the prediction of the biological market theory that variation in a group's dominance gradient will influence the patterns of reciprocity and interchange of grooming and prosocial behaviour (i.e., punishment).

4. To test the Covariation hypothesis prediction that the patterns of conflict management tend to be intercorrelated and are related to the group's dominance style and hierarchy steepness.

5. To test the prediction of the Relational model that individuals that have participated in an agonistic encounter are likely to switch their aggressive motivation to an affiliative mode and engage in affiliative behaviour right after the conflict has ended.

# CHAPTER 2

# Activity time budgets, sociality and gregariousness in geladas (*Theropithecus gelada*) and mandrills (*Mandrillus sphinx*): A comparative study

**Abstract.** Primates spend their daytime engaged in four time-consuming, biologically relevant activities, namely, moving, resting, foraging, and socializing (this includes affiliative, aggressive and play behaviours). On the other hand, socio-spatial behaviour is known to be a basic index of a group's social structure. Evolutionary theory claims that natural selection should be expected to shape the individuals' time budget allocation decisions and their socio-spatial arrangements so as to maximize their fitness, that is, they both should be flexibly adjusted to current local conditions. Here we analyse time budgets and socio-spatial behaviour (assessed at four social distances) of a group of geladas and a group of mandrills that were housed in similarly naturalized and sized enclosures, were exposed to identical local weather conditions, and were food-provisioned and predation free. We aimed to further our understanding of how individuals and groups belonging to different species schedule their activity budgets and organize their socio-spatial patterns of sociality and gregariousness in an especially relaxed ecological setting. Our findings showed that their time budgets fell well within the range of variation found for wild populations of *Papio* and *Theropithecus* baboons. They also showed that at close distance the study individuals spent most of their time alone and, when accompanied, they tended to form small cliques made of just one or two neighbours (duos and trios). Although the two study groups shared a similar ecological setting and shared *overall patterns* of time budgets, sociality and gregariousness, however, they still were found to significantly differ in the amount of time they invested in each behavioural activity and in the amount of time they were alone (sociality) and accompanied by a varying number of neighbours (gregariousness). Overall, geladas were found to be more sociable and gregarious and to keep higher levels of social time than mandrills.

**Keywords.** Activity budgets, socio-spatial behaviour, sociality, gregariousness, gelada, mandrill

## Introduction

Most primates are diurnal (Martin, 1990; Nystrom and Ashmore, 2008) and spend their daylight hours engaged in a variety of time-consuming, biologically relevant activities that have conventionally been classified into four mutually exclusive categories: moving/travelling, resting, feeding/foraging, and socializing (Altmann, 1980, Altmann and Muruthi, 1988; Bronikowski and Altmann, 1996; Dunbar, 1988, 1992a, 1992b, Dunbar, Korstjens, and Lehmann, 2009; Hill, 2006, Hill *et al.,* 2003; Sussman, *et al.*, 2003, Sussman and Garber, 2011; van Doorn, O'Riain and Swedell, 2009). In some studies, the behavioural category labelled socializing (or social time) is further broken down into several components, such as aggression, affiliation (huddling, grooming) and play (e.g., Bernstein, 1970, 1975, 1976, 1980, 1988; Filipcik *et al.*, 2014; Jaman and Huffman, 2008, 2013; Sussman *et al.*, 2003, Sussman and Garber, 2011). Evolutionary theory dictates that the allocation of the limited time available to engage in these various non-overlapping activity categories is unlikely to be random, as they significantly impact the individuals' ability to maximize their survival and reproduction (Dunbar, 1988; Dunbar *et al.*, 2009; Hill and Dunbar, 2002; Korstjens, Lehmann and Dunbar, 2010). Accordingly, it has been argued that natural selection is expected to shape the individuals' time budget allocation decisions so as to maximize their fitness, that is, they should spend more time in those activities that yield the highest payoffs. And this is achieved by adjusting the time budgets to their energy requirements related to life history (e.g., body size, age, and reproductive condition), to their psychological and social needs (e.g., emotional and social support), and to the biotic and abiotic environmental conditions that they encounter (e.g., temperature, length of daylight, predatory pressure, group size, distribution and abundance of food, diet type) (Bronikowski and Altmann, 1996; Dunbar, 1988, 1992a, 1992b; Hill, 2006, Hill *et al.,* 2003; Majolo, Vizioli and Schino, 2008; van Doorn *et al.*, 2009).

A central issue in life history theory is that the various activity categories cannot be time-shared. Increased time budgets on a given activity occur at the expense of time spent on other activities (Stearns, 1989). That is, the various activity categories are antagonistic in the sense that they compete for the finite time and energy budget that individuals can apportion. In other words, individuals face tradeoffs between the various activities. Thus, the study of variation in activity budgets under different environmental conditions can potentially provide an opportunity to identify some of the key factors that account for much of such variation. Unfortunately, detailed information on the activity budgets of primates in the wild and in captivity is largely lacking or incomplete for many taxa (see, however, Majolo *et al.*, 2008; Dunbar *et al.*, 2009; Flashing, 2011; Sussman and Garber, 2011; Swedell, 2011 for reviews). This precludes a fully productive use of comparative studies aimed to analyse the variation in activity budgets by populations of individuals of the *same species* exposed to *different* and *similar* environmental conditions and by individuals of *different species* exposed to *similar* environmental conditions. The latter is our main concern in the present study.

Several authors have adopted a modelling approach to identify the factors that account for the variation reported in the time budgets allocated to several activity categories in wild populations of a number of species of cercopithecoids and hominoids (reviews in Dunba *et al.*, 2009; Lehmann, Korstjens, and Dunbar, 2007, 2008, 2010). Overall, the main conclusions from these studies can be spelled out as follows: (1) ambient temperature influences the distribution and abundance of food, (2) in turn, the latter effect influences the group's size (and coherence) and length of the daily foraging march (i.e., home range and geographical distribution), and (3) these effects place serious constraints on the time available to adequately budget the various behavioural activities, including the servicing of the individuals' fitness-enhancing social relationships with group members (i.e., friendships and alliances). Among the species of cercopithecoids that have provided the most illuminating empirical tests of these models are the savanna baboon, *Papio* spp. (Bronikowski and Altmann, 1996; Hill *et al.*, 2003; Hill, 2006), and the gelada or montane baboon, *Theropithecus gelada* (Dunbar, 1992a, 1992b), one of the two species in the present study. Regretfully, no comparable data are available for the other species studied in the present research, the mandrill, *Mandrillus sphinx* (Swedell, 2011), also called the forest baboon (Stambach, 1987). At most, a few field studies have confirmed the expected positive relation between home range size and group size in this species (White, 2010; Brockmeyer *et al.*, 2015).

Studies of activity budgets in captive settings are meagre. Over a period of about twenty-five years (1963-1988), Bernstein published a series of reports on the activity budgets of several species of primates housed in group-living conditions in nearly-identical outdoor compounds: *Macaca mulatta* (Bernstein and Mason, 1963), *M. nemestrina* (Bernstein, 1970), *Theropithecus gelada* (Bernstein, 1975), *Cercocebus atys* (Bernstein, 1976), *M. arctoides* (Bernstein, 1980), and *M. nigra* (Bernstein, 1988). More recently, Jaman and Huffman (2008) compared the activity budgets of groups of Japanese macaques housed in vegetated and nonvegetated enclosures. These studies are thus relevant to the general issue, tackled in the present study, of how current ecological conditions and evolutionary history account for the observed between species variation in activity profiles (Chapman and Rothman, 2009; Di Fiore and Rendall, 1994; Rendall and Di Fiore, 2007; Strier, Lee and Ives, 2014; Thierry, 2007, Thierry, Iwaniuk and Pellis, 2000).

One of the basic approaches to the study of social structure concerns the analysis of socio-spatial behaviour, that is, of how group members associate with one another and form stable subgroups, cliques or social networks of variable cohesion and temporal stability (Bret *et al.,* 2013; Corradino, 1990; Cowlishaw, 1999; Ehardt-Seward and Bramblett, 1980; Fairbanks, 1976; Hornshaw, 1984; Pasquaretta *et al.,* 2014). And the study of how individuals use their social niche, that is, their patterns of social proximity to one another is the second topic we will tackle in the present study. In the approach adopted here to studying socio-spatial behaviour, the basic datum of interest is "who is with whom". This is further enriched by assessing this information at several social distances, from one indicating the strongest intimacy, when the individuals are in actual physical contact with one another (e.g., huddling or contact sitting), up to another reflecting a rather loose, but still relatively individualized spatial association, when the individuals are, for example, within each other's circle of four meters. So the general question we set out to analyse in this context is how much time each and every individual spends with each other within four categories of social distance. We are interested in determining how much time they spend with others *versus* alone (in each distance category), and, when they are with someone else, how many others are around (in each distance analysed) at the same time (i.e., clique size).

The objective of this comparative study of activity budgets and socio-spatial behaviour of a group of geladas and a group of mandrills housed in rather similar naturalistic enclosures and food-provisioned and predation free is twofold. First, we want to explore what happens when individuals are freed from the time constraints and energy demands that operate in the wild (see Polo and Colmenares, 2016). Thus, if, as predicted by socioecological theory (Clutton-Brock and Janson, 2012; Koenig *et al.,* 2013; Parga and Overdorff, 2011; Thierry, 2013; van Schaik, 2016), the individuals' activity time budgets are shaped by ecological, demographic, social, and biological (life-history) factors, then in food provisioned groups we should expect a significant relaxation of the impact of these factors, as individuals do not have to spend much time and energy in travelling for food, i.e., foraging and moving (Altmann and Muruthi, 1988, Altmann and Alberts, 2003; Jaman and Huffman, 2013). The enclosures of our two study groups were vegetated, so we had an opportunity to see if this one factor, along with the fact that they both were food provisioned, had a significant effect on the distribution of their time budgets, and if any species differences in such similar ecological conditions arose (see also Jaman and

Huffman, 2008). The issue of how captivity affects the behaviour of primates has been assessed on a number of occasions (see de Waal, 1989, de Waal, Aureli and Judge, 2000; Judge, 2000 for reviews), with an emphasis placed on the study of the coping strategies that individuals activate under different conditions of short-term and long-term social or spatial density. One major conclusion from these studies is that the relation between density (due to captivity) and behaviour, not just aggression, is far from simple.

The second objective involved a fine-grained analysis of socio-spatial behaviour in the two study groups. We looked to see the extent that the differences in the organization of their social niches that have been documented to exist in the wild for the two species (gelada: Dunbar, 1984, 1992a; Kawai *et al.,* 1983; Snyder-Mackler *et al.,* 2012; mandrill: Dixon, Bossi, and Wickings, 1993; Grueter, Chapais and Zinner, 2012; Setchell and Wickings, 2005; see Swedell, 2011, for a review) still emerge when they are food provisioned and housed in similar naturalistic enclosures.

## Material and Methods

### *Study groups and housing*

The present study was conducted from October 2010 until April 2011 at La Vallée des Singes, a large monkey and ape park located in Romagne (France). Subjects were the members of two groups of cercopithecoid African papionins, *Theropithecus gelada* and *Mandrillus sphinx* (Table 2.1), housed in roughly similar naturalistic settings in captivity.

**Table 2.1.** Subjects of Study*

| **Individual**[1] | **Species** | **Sex** | **Age Class**[2] | **Observations** |
|---|---|---|---|---|
| Bongo (B) | Gelada | M | Adult (7) | Alpha male. Father of Saala, Dashan, Lengay and Haile |
| Lena (L) | Gelada | F | Adult (12) | Alpha female. Mother of Axoun, Saala and Lengay |
| Axoun (AX) | Gelada | M | Subadult (5) | |
| Saala (S) | Gelada | F | Juvenile (3) | |
| Ute (U) | Gelada | F | Adult (11) | Mother of Okoume, Dashan and Haile |
| Okoume (OK) | Gelada | M | Subadult (5) | |
| Dashan (D) | Gelada | M | Juvenile (3) | |
| Haile (H) | Gelada | F | Yearling (1) | |
| Lengay (LG) | Gelada | M | Infant (0.4) | |
| Zoulou (Z) | Mandrill | M | Adult (17) | Alpha male. Father of Amala, Mpassa, Mambassa, Okandja, Nouanda, Nyombé, Lekedi, Mboko, Ebaka, Leny, Natiwe and Mkoa |
| Nina (N) | Mandrill | F | Adult (16) | Alpha female. Mother of Amala, Mpassa, Mambassa, Okandja and Nouanda |
| Nouanda (NO) | Mandrill | F | Adult (9) | |
| Mambassa (MA) | Mandrill | F | Adult (7) | |
| Okandja (OK) | Mandrill | M | Subadult (6) | |
| Mpassa (MP) | Mandrill | F | Adult (5) | |
| Amala (AM) | Mandrill | F | Subadult (4) | |
| Nicky (NI) | Mandrill | F | Adult (14) | Mother of Nyombe, Lekedi and Natiwe |
| Nyombe (NY) | Mandrill | F | Adult (9) | |
| Lekedi (LK) | Mandrill | M | Subadult (6) | |
| Csilla (CS) | Mandrill | F | Adult (14) | Mother of Mboko, Ebaka, Leny and Mkoa |
| Ebaka (EB) | Mandrill | F | Adult (9) | |
| Mboko (MB) | Mandrill | M | Subadult (8) | |
| Leny (LE) | Mandrill | F | Subadult (4) | |
| Nico (NC) | Mandrill | M | Adult (12) | |
| Natiwe (NAT) | Mandrill | F | Infant (1) | |
| Mkoa (MK) | Mandrill | F | Infant (1) | |

*Sources: Charpentier *et al.* (2004); Dunbar (1980); Dunbar & Dunbar (1975); Kawai *et al.* (1983); Laidre & Yorzinski (2005); Leone & Palagi (2010).

[1] Code name in parentheses

[2] Years of age in parentheses

The group of geladas was made up of 9 individuals: one adult male, two adult females, two subadult males, one juvenile male, one juvenile female, one yearling female and one infant male. The group of mandrills comprised 17 individuals: two adult males, eight adult females, three subadult males, two subadult females, and two infant females. The two groups' enclosures consisted of an indoor facility, not visible to visitors, and a large outdoor compound. They included live and dead trees, big rocks, dens, wooden structures built with trunks placed in different positions and interconnected at different levels (Fig. 2.1). The geladas' indoor area was divided into five interconnected rooms,

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**Figure 2.1** Views of (a) gelada and (b) mandrill naturalistic enclosures at La Vallée des Singes.

5.30m x 5.80m. It was connected through a hatch system, which was always opened during the periods of data collection, to a 2,800m$^2$ outdoor exhibit surrounded by a water moat and visible to visitors. This open-air outdoor compound, which circled the indoor zone, had predominantly herbaceous vegetation with several trees and a wooden structure 4 meters high and 15 meters long. The mandrills' indoor area was also divided into five inter-connected rooms, 16.80m x 12.10m with several wooden structures. It was connected through a hatch system, also opened during the sessions of data collection, to a 3,500m$^2$ outdoor exhibit, visible to visitors and surrounded by a water moat and the indoor area.

This open-air outdoor area was densely vegetated (shrubs and trees) and included wooden structures and platforms above the ground.

In addition to the vegetation available in the enclosures that the individuals of both groups could and did consume *ad libitum*, geladas were fed four times per day (8.45 a.m., 11.45 a.m., 2.30 p.m. and 4 p.m.), and their diet included grass, vegetables, grains and pellets. Mandrills were fed six times per day (8.30 a.m., 12 a.m., 2.30 p.m., 3.30 p.m., 4.30 p.m. and 5.30p.m.); their diet included fruits, nuts, vegetables, grains and pellets. For both species water was always available *ad libitum*.

*Data collection: behavioural catalogue, and sampling and recording methods*

The catalogue of *behavioural activity* categories used in this study included those that are traditionally recorded in studies of activity budgets in primates in general (see above: Introduction) and in geladas and mandrills in particular (gelada: Dunbar, 1992a; Bernstein, 1975; mandrill: Brockmeyer *et al.,* 2015; Chang, Forthman, and Maple, 1999), that is, *foraging/feeding* (F), *moving/traveling* (M), *resting* (R), and *socializing* (S). Socializing was further divided into three subcategories, namely, affiliation (AF), aggression (AG), and social play (SP) (gelada: Bernstein, 1975; Dunbar and Dunbar, 1975; Mancini and Palagi, 2009; mandrill: Brockmeyer *et al.,* 2015; Chang *et al.,* 1999; Feistner, 1989; Mellen *et al.*, 1981). A number of social distance categories were also established, namely, C, $P_1$, $P_2$ and $P_3$; they are defined in Table 2.2. Spacing behaviour has also been studied in geladas (Dunbar, 1983; Kawai and Mori, 1979), but not in mandrills, although none of these few studies have used metrics that match the one used in the present study.

**Table 2.2** Social distance categories and its definitions

| Category | Definition |
|---|---|
| C | In contact with other individual |
| P1 | Within one arm's reach from other individual |
| P2 | Between one and two arms' reach from other individual |
| P3 | Between two arms and four meters away from other individual |

The behavioural data analysed in this chapter, i.e., categories of behavioural and social activities and of social-spatial behaviour were sampled via focal-group sampling (for geladas: N= 7) and focal-animal sampling (for mandrills: N= 15). The observations were directly recorded on previously designed check sheets using instantaneous (or point) sampling every 10 minutes (Altmann, 1974; Dunbar, 1976; Lehner, 1996; Martin and Bateson, 2007). All the records included information about the behavioural (and social) activity that the focal subject(s) was engaged in, as well as the identity of the individuals (i.e., neighbours) that were within each one of the four social distance categories defined (Table 2.2), that is, in contact, and at $P_1$, $P_2$ and $P_3$. We recorded a total of 835 group scans (point samples) and 818 individual scans (point samples) in the gelada and mandrill groups, respectively. In each group, individuals younger than 1.5 years of age were never sampled.

### *Behavioural measures and data analyses*

The records used to analyse activity budgets were transformed into percentages of sample points that each individual had spent in each activity category: F, M, R, and S. When the subject was engaged in a social interaction (S for socializing), then the record further specified if the behaviour was affiliative (AF), aggressive (AG) or play (SP). In order to compare our results on activity budgets with those from other studies we run two separate analyses. First, we analysed the four general categories of activity budgets, foraging/feeding, moving/traveling, resting and socializing. The second analysis focused on the three components that make up the category socializing, that is, affiliation, aggression, and social play. Since sample sizes were small (N= 7 geladas and N= 15 mandrills), we used non-parametric statistics (Siegel and Castellan, 1988; Neave and Worthington, 1988; Zar, 1999; Hawkins, 2005) to run all the analyses on activity budgets. We used one-way non-parametric Friedman ANOVAs to study the variation in the time (i.e., % of sample points) that individuals spent in each behavioural category. If this Friedman test yielded statistically significant differences, then post-hoc pairwise comparisons were conducted via Wilcoxon signed-rank tests. In all the comparisons of geladas *versus* mandrills (two unrelated samples) we used the Mann-Whitney U test.

From the records on socio-spatial behaviour two behavioural measures were worked out. First, we defined two socio-spatial measures, sociality and gregariousness (Colmenares, unpublished) and examined them at each of the four proximity categories recorded (i.e., C, $P_1$, $P_2$ and $P_3$). S*ociality* was defined as the percentage of sample points each individual was accompanied across the four social distance categories. This index provides aggregated information across ‘rings’ (i.e., each social distance category) on how often the individuals were accompanied (not alone). Therefore, this index deals with ‘discs’, not ‘rings’, of increasingly greater social distance (Figure 2.2). *Gregariousness* was defined as the percent of sample points each individual was surrounded by one (was in a duo), two (was in a trio), three (was in a quartet), four (was in a quintet) or more group partners. It turned up that individuals were rarely found to be surrounded by more than 2 or 3 neighbours and this occurred only at the farthest distance ($P_3$). This index thus provides information about how many group partners were around each individual at each of the four distance categories and, like sociality, it also deals with ‘discs’, not ‘rings’, as the information on each distance is aggregated from contact up to $P_3$. In these analyses of socio-spatial behaviour one-way non-parametric Friedman ANOVAs were also used to study the variation in sociality across the four social distance categories; and Wilcoxon signed-rank tests were used in pairwise post-hoc planned comparisons and in comparisons involving just two related samples. Except for the pairwise comparisons, where Bonferroni criterion was used to adjust p- values, the significance level was set at $p < 5\%$. We used SPSS version 20 to run all the analyses. In all the comparisons of socio-spatial behaviour between geladas and mandrills (two unrelated samples) Mann-Whitney U tests were used.

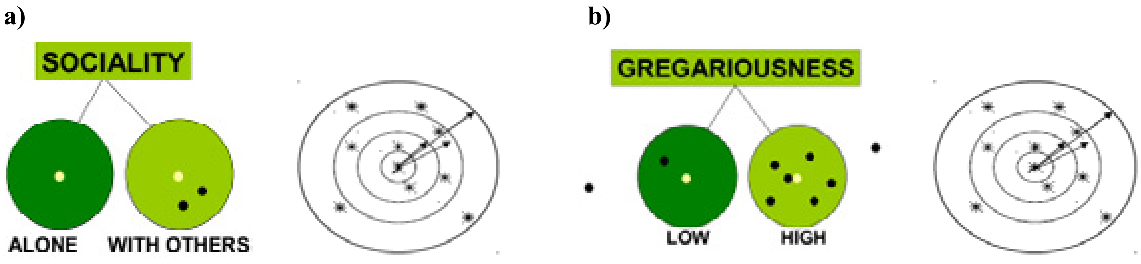


**Figure 2.2** Graphical depiction of the two measures of socio-spatial behaviour analysed, (a) sociality, and (b) gregariousness.

## Results

### *Activity budgets*

The time geladas spent in the four categories of Behavioural Activity, i.e., *Foraging*, *Moving*, *Resting*, and *Socializing*, was significantly unequal ($\chi2(3) = 19.35$, N= 7; $p < 0.001$; Fig. 2.3). They clearly privileged *Foraging* over the other three activity categories (Table 2.3), although in the pairwise comparisons between the four categories with the level of significance adjusted with Bonferroni correction, the only difference that reached statistical significance was between *Moving* and *Foraging* (7.5 *versus* 55.6%, $z = 3$, $p < 0.001$; Table 2.3). In the analysis of the categories of Social Activity, i.e., *Affiliation*, *Aggression*, and *Social Play*, the time they spent in each of the three categories was significantly unequal ($\chi2(2) = 12$, N= 7; $p = 0.002$; Fig. 2.4). Of the three social categories, they were found to engage more often in *Affiliation* than *Play* (87.4 *versus* 11.6%, $z = 1.29$; $p = 0.048$; Table 2.3), and *Aggression* (87.4 *versus* 1%, $z = 1.71$; $p = 0.004$; Table 2.3).

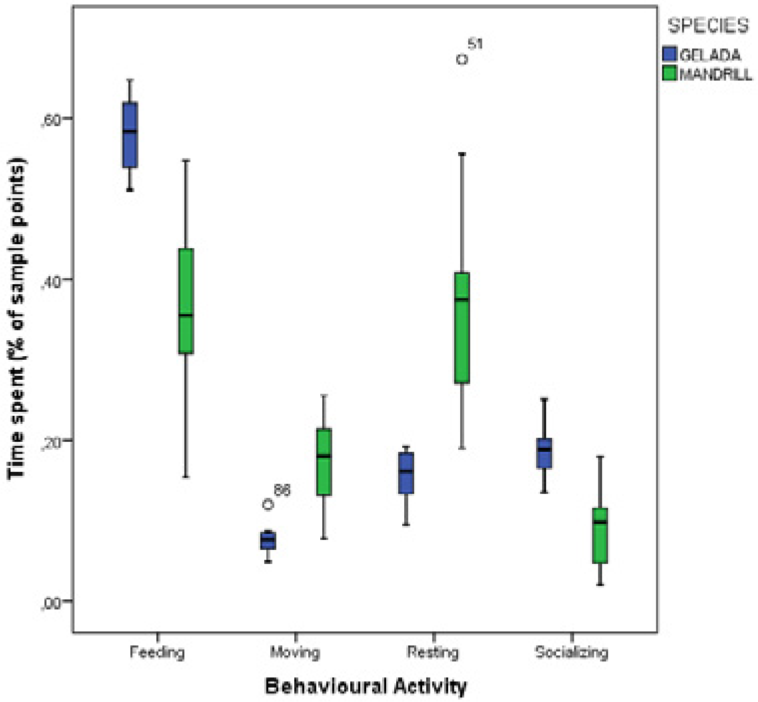


**Figure 2.3** Comparison of time budgets in each activity category in geladas *versus* mandrills: foraging/feeding, moving, resting and socializing. The box plots represent medians (black horizontal lines), interquartile range (boxes), minima and maxima (whiskers) as well as outliers (circles).

**Table 2.3** Activity budgets of geladas (% sample intervals)

| Individual | M | F | R | S | AF | AG | SP |
|---|---|---|---|---|---|---|---|
| B | 4.69 | 48.55 | 17.93 | 23.86 | 99.42 | 0.58 | 0.00 |
| L | 7.53 | 52.97 | 17.44 | 19.82 | 100.00 | 0.00 | 0.00 |
| AX | 7.99 | 51.26 | 18.38 | 18.11 | 80.88 | 2.94 | 16.18 |
| S | 8.39 | 60.25 | 10.87 | 16.92 | 82.93 | 0.81 | 16.26 |
| U | 5.31 | 61.77 | 9.12 | 19.18 | 100.00 | 0.00 | 0.00 |
| OK | 7.23 | 58.25 | 14.73 | 14.73 | 85.19 | 2.78 | 12.04 |
| D | 11.50 | 55.89 | 15.43 | 12.99 | 63.54 | 0.00 | 36.46 |
| **Mean** | **7.52** | **55.56** | **14.84** | **17.94** | **87.42** | **1.02** | **11.56** |
| **Median** | **7.53** | **55.89** | **15.43** | **18.11** | **85.19** | **0.58** | **12.04** |
| **SD** | 2.23 | 4.87 | 3.60 | 3.56 | 13.53 | 1.30 | 13.32 |
| **SEM** | 0.84 | 1.84 | 1.36 | 1.35 | 5.11 | 0.49 | 5.03 |

M: moving/travelling; R: resting; F: foraging/feeding; AF: affiliation; AG: aggression; SP: social play.

The time mandrills spent in the four activity categories, i.e., *Foraging*, *Moving*, *Resting*, and *Socializing*, was also significantly unequal ($\chi2(3) = 36.1$, N= 15, $p < 0.001$; Fig. 2.3). In the pairwise comparisons, statistically significant differences were found between *Foraging* and *Moving* (33.6 *versus* 15.5%, z = 1.53; p = 0.007; Table 2.4), *Foraging* and *Socializing* (33.6 *versus* 8.5%, z = 2.46; $p < 0.001$; Table 2.4), *Moving* and *Resting* (15.5 *versus* 33.9%, z = -1.27; p = 0.043; Table 2.4), and *Resting* and *Socializing* (33.9 *versus* 8.5%, z = 2.2; $p < 0.001$; Table 2.4). In the analysis of the categories of Social Activity, i.e., *Affiliation*, *Aggression*, and *Social Play*, the time they invested in each of the three categories was found to be significantly unequal ($\chi2(2) = 26.93$, N= 15; $p < 0.001$; Fig. 2.4). Of the three social categories, they engaged more often in *Affiliation* than *Play* (94.4 *versus* 4.3%, z = 1.4; $p < 0.001$; Table 2.4), and *Aggression* (94.4 *versus* 1.33%, z = 1.5; $p < 0.001$; Table 2.4).

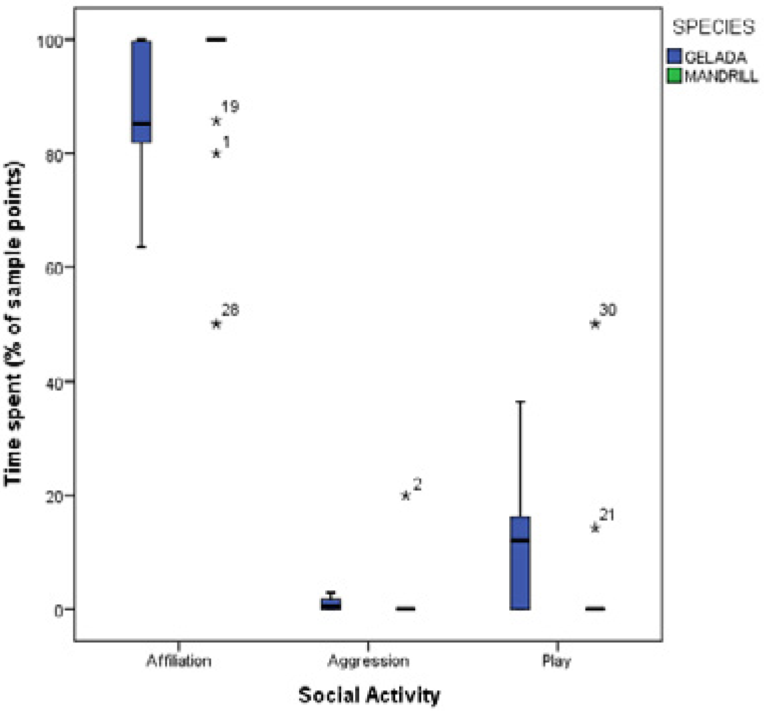


**Figure 2.4** Comparison of time budgets in each component of the category of behavioural activity SOCIAL in geladas *versus* mandrills: affiliation, aggression, and play. The box plots represent medians (black horizontal lines), interquartile range (boxes), minima and maxima (whiskers) as well as outliers (asterisks).

**Table 2.4** Activity budgets of mandrills (% sample intervals)

| Individual | M | F | R | S | AF | AG | SP |
|---|---|---|---|---|---|---|---|
| Z | 10.00 | 20.00 | 48.00 | 10.00 | 80.00 | 20.00 | 0.00 |
| N | 12.96 | 24.07 | 55.56 | 7.41 | 100.00 | 0.00 | 0.00 |
| NO | 7.41 | 46.30 | 33.33 | 1.85 | 100.00 | 0.00 | 0.00 |
| MA | 18.00 | 50.00 | 28.00 | 4.00 | 100.00 | 0.00 | 0.00 |
| OK | 12.00 | 46.00 | 22.00 | 4.00 | 100.00 | 0.00 | 0.00 |
| MP | 22.22 | 40.00 | 17.78 | 13.33 | 100.00 | 0.00 | 0.00 |
| AM | 18.60 | 27.91 | 27.91 | 16.28 | 85.71 | 0.00 | 14.29 |
| NI | 7.41 | 38.89 | 37.04 | 11.11 | 100.00 | 0.00 | 0.00 |
| NY | 16.00 | 26.00 | 34.00 | 8.00 | 100.00 | 0.00 | 0.00 |
| LK | 22.22 | 40.00 | 26.67 | 4.44 | 50.00 | 0.00 | 50.00 |
| CS | 17.54 | 29.82 | 38.60 | 10.53 | 100.00 | 0.00 | 0.00 |
| EB | 17.54 | 28.07 | 19.30 | 14.04 | 100.00 | 0.00 | 0.00 |
| MB | 12.73 | 14.55 | 63.64 | 3.64 | 100.00 | 0.00 | 0.00 |
| LE | 23.08 | 40.38 | 17.31 | 9.62 | 100.00 | 0.00 | 0.00 |
| NC | 14.81 | 31.48 | 38.89 | 9.26 | 100.00 | 0.00 | 0.00 |
| **Mean** | **15.50** | **33.56** | **33.87** | **8.50** | **94.38** | **1.33** | **4.29** |
| **Median** | **16.00** | **31.48** | **33.33** | **9.26** | **100.00** | **0.00** | **0.00** |
| **SD** | 5.07 | 10.41 | 13.69 | 4.27 | 13.71 | 5.16 | 13.17 |
| **SEM** | 1.31 | 2.69 | 3.53 | 1.10 | 3.54 | 1.33 | 3.40 |

M: moving/travelling; R: resting; F: foraging/feeding; AF: affiliation; AG: aggression; SP: social play.

Geladas spent more time than mandrills in *Foraging* (55.6 *versus* 33.6%, respectively; Mann-Whitney U test, $U = 101$, $z = 3.420$, $p < 0.001$; Fig. 2.3) and *Socializing* (17.9 *versus* 8.5%, respectively; $U = 98$, $z = 3.208$, $p < 0.001$; Fig. 2.3); however, the latter scored higher than geladas in *Moving* (15.5 *versus* 7.5%, respectively; $U = 7$, $z = 3.208$, $p < 0.001$; Fig. 2.3), and *Resting* (33.9 *versus* 14.84%, respectively; $U = 2$, $z = 3.560$, $p < 0.001$; Fig. 2.3). Mandrills scored higher than geladas in *Affiliation* and *Aggression* (affiliation: 94.4 *versus* 87.5%, respectively; $U = 28$, $z = -2.003$, $p = 0.046$; aggression: 1.33 *versus* 1%, respectively; $U = 28$, $z = -2.352$, $p = 0.021$; Fig. 2.4), however, geladas scored higher than mandrills in *Play* (11.6 *versus* 4.3%, respectively, $U = 30.5$, $z = -1.976$, $p = 0.040$; Fig. 2.4).

Whereas the predominant Behavioural Activity in geladas was *Foraging* (55.6%, Table 2.3), in mandrills, in contrast, it was *Resting* and *Foraging* (33.9 and 33.6%, respectively; Table 2.4). In geladas, the Behavioural Activity in which they spent least was *Moving* (7.5 %, Table 2.3), whereas in mandrills it was *Socializing* (8.5%; Table 2.4). With regards to the time engaged in the three Social Activities analysed, in both species *Affiliation* was the predominant activity (87.4 and 94.3%, geladas and mandrills, respectively, Tables 2.3 and 2.4), followed by *Play* (11.56 and 4.29%, respectively, Tables 2.3 and 2.4) and then *Aggression* (1 and 1.33%, respectively, Tables 2.3 and 2.4).

*Socio-spatial Behaviour*

In both species, *sociality* (% of time with someone around) tended to increase as the social distance increased, although this pattern was clearer in geladas than mandrills (geladas: $\chi2(3) = 21$, N= 7; $p < 0.001$; mandrills: $\chi2(3) = 42.6$, N= 15; $p < 0.001$; Fig. 2.5). Also, in both species the abrupt change upward occurred at the farthest distance category (P2 vs P3: 39.1 *versus* 78.4% and 19.7 *versus* 68%, geladas *versus* mandrills, respectively; Tables 2.5-2.6). In three of the four social distance categories analysed, geladas had higher scores of sociality than mandrills did (C: 24.3 *versus* 8%, $U = 0$, $z = -3.7$, $p < 0.001$; $P_1$: 33 *versus* 16.7%, $U = 2.5$, $z = -3.53$, $p < 0.001$; $P_2$: 39.1 *versus* 19.7%, $U = 8$, $z = -3.13$, $p = 0.001$; $P_3$: 78.4 *versus* 68%, $U = 26$, $z = -1.87$, $p = 0.07$, NS; Fig. 2.5; Tables 2.5-2.6).

Geladas spent much *time alone* ( > 50%; Table 2.7) at the three first categories of social distance (C: 75.6%; $P_1$: 68%; $P_2$: 60.8 %). Only at the farthest distance category, their time alone dropped dramatically (60.8 *versus* 21.6, $z = -2.37$, $p = 0.016$; Table 2.7). A rather similar pattern in *time alone* was found in mandrills (C: 92.2%; $P_1$: 83.2%; $P_2$: 80.3%; Table 2.8), with the drop also occurring at $P_3$ (80.3 *versus* 31.9, $z = -3.41$, $p < 0.001$; Table 2.8).

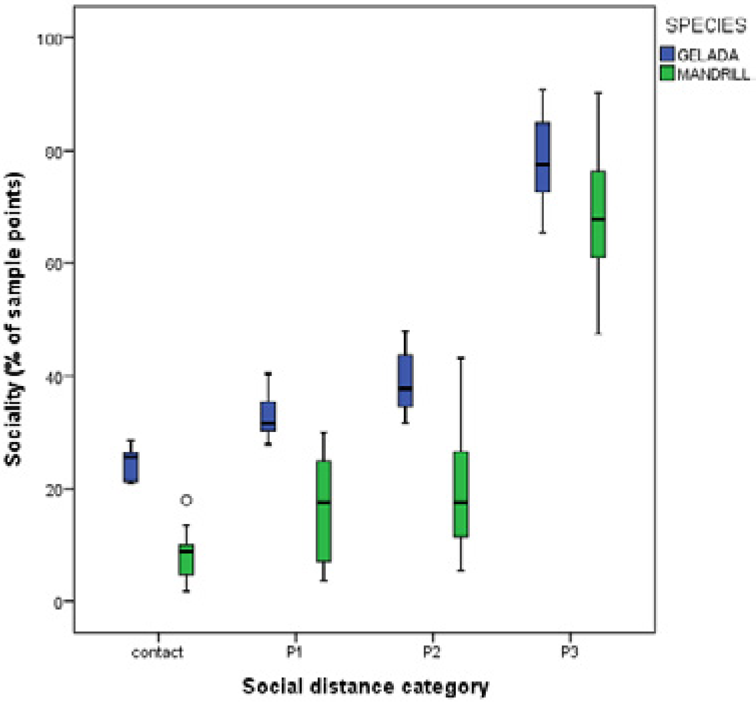


**Figure 2.5** Sociality in geladas *versus* mandrills, in the four distance categories: contact, within one arm's reach, between one and two arms' reach, between two arms' reach and four meters. The box plots represent medians (black horizontal lines), interquartile range (boxes), minima and maxima (whiskers) as well as outliers (circles).

**Table 2.5** Scores of sociality of geladas (% sample intervals)*

| Individual | C | P1 | P2 | P3 |
|---|---|---|---|---|
| B | 26.87 | 29.55 | 32.75 | 65.37 |
| L | 28.57 | 40.39 | 47.92 | 84.03 |
| AX | 25.58 | 35.73 | 41.52 | 77.51 |
| S | 21.37 | 35.09 | 45.91 | 90.77 |
| U | 25.83 | 31.66 | 36.29 | 75.76 |
| OK | 21.27 | 27.87 | 31.70 | 69.48 |
| D | 20.96 | 31.05 | 37.77 | 85.77 |
| **Mean** | **24.35** | **33.05** | **39.12** | **78.38** |
| **Median** | **25.58** | **31.66** | **37.77** | **77.51** |
| **SD** | 3.10 | 4.29 | 6.25 | 9.09 |
| **SEM** | 1.17 | 1.62 | 2.36 | 3.44 |

*Scores are % of sample intervals that individuals spent with at least one neighbour (i.e. not alone) at each social distance category (C, P1, P2 and P3).

**Table 2.6** Scores of sociality of mandrills (% sample intervals)*

| **Individual** | C | **P1** | **P2** | **P3** |
|---|---|---|---|---|
| Z | 7.84 | 27.45 | 43.14 | 90.20 |
| N | 9.26 | 29.63 | 37.04 | 88.89 |
| NO | 5.45 | 5.45 | 10.91 | 52.73 |
| MA | 1.75 | 7.02 | 12.28 | 66.67 |
| OK | 3.77 | 5.66 | 9.43 | 62.26 |
| MP | 18.00 | 18.00 | 24.00 | 72.00 |
| AM | 13.21 | 22.64 | 30.19 | 83.02 |
| NI | 8.77 | 17.54 | 17.54 | 50.88 |
| NY | 4.00 | 30.00 | 12.00 | 62.00 |
| LK | 1.82 | 3.64 | 5.45 | 60.00 |
| CS | 10.53 | 17.54 | 19.30 | 47.37 |
| EB | 13.56 | 27.12 | 27.12 | 67.80 |
| MB | 5.26 | 7.02 | 8.77 | 80.70 |
| LE | 8.93 | 12.50 | 12.50 | 67.86 |
| NC | 9.26 | 20.37 | 25.93 | 68.52 |
| **Mean** | **8.09** | **16.77** | **19.71** | **68.06** |
| **Median** | **8.77** | **17.54** | **17.54** | **67.80** |
| **SD** | 4.58 | 9.43 | 11.17 | 13.14 |
| **SEM** | 1.18 | 2.43 | 2.89 | 3.39 |

*Scores are % of sample intervals that individuals spent with at least one neighbour (i.e. not alone) at each social distance category (C, P1, P2 and P3).

In geladas, the individuals spent significantly more time alone than with just one neighbour [duos] at C, $P_1$ and $P_2$ ($z = -2.37$, $p = 0.016$, and all cases; Table 2.7). This pattern only changed at $P_3$, where the difference was no longer significant (21.6 *versus* 31.3%, $z = -2.03$, $p > 0.025$, NS; Table 2.7). At $P_3$, the cut-off point was between trios and quartets (23.7 *versus* 10.6%, respectively, $z = -2.37$, $p = 0.016$; Table 2.7). The very same patterns were found in mandrills. They spent significantly more time alone than in duos (i.e., one neighbour) at C, $P_1$ and $P_2$ ($z = -3.41$, $p < 0.001$, and all cases; Table 2.8), but not at $P_3$ (31.9 *versus* 36.6%, $z = -1.13$, $p > 0.025$, NS; Table 2.8). Like in geladas, the cut-off point was between trios and quartets (23.3 *versus* 6.53%, respectively, $z = -3.41$, $p < 0.001$; Table 2.8).

**Table 2.7** Scores of gregariousness of geladas (% sample intervals)*

| | **Contact** | | | | | **P1** | | | | | **P2** | | | | | **P3** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Individual** | **0** | **1** | **2** | **3** | **4** | **0** | **1** | **2** | **3** | **4** | **0** | **1** | **2** | **3** | **4** | **0** | **1** | **2** | **3** | **4** |
| B | 73.13 | 26.60 | 0.27 | 0.00 | 0.00 | 70.45 | 28.61 | 0.80 | 0.13 | 0.00 | 67.25 | 30.35 | 2.14 | 0.27 | 0.00 | 34.63 | 37.30 | 14.30 | 4.28 | 2.27 |
| L | 71.30 | 22.21 | 2.34 | 1.43 | 1.95 | 59.74 | 30.52 | 5.32 | 1.95 | 1.82 | 52.08 | 34.94 | 8.18 | 1.69 | 2.34 | 15.97 | 26.88 | 29.22 | 13.64 | 6.23 |
| AX | 74.29 | 22.24 | 1.80 | 0.51 | 1.03 | 64.27 | 27.63 | 5.78 | 0.64 | 1.03 | 58.48 | 30.59 | 8.10 | 0.64 | 1.67 | 22.49 | 28.15 | 24.42 | 11.57 | 5.91 |
| S | 78.63 | 15.83 | 2.77 | 1.45 | 1.32 | 64.91 | 24.67 | 6.33 | 2.11 | 1.58 | 54.09 | 32.59 | 8.18 | 2.37 | 2.11 | 9.23 | 29.16 | 34.04 | 13.85 | 6.33 |
| U | 74.17 | 21.72 | 1.59 | 1.46 | 1.06 | 68.34 | 25.56 | 3.31 | 1.46 | 0.93 | 63.71 | 29.01 | 4.11 | 1.59 | 0.93 | 24.24 | 40.53 | 15.89 | 7.42 | 3.97 |
| OK | 78.73 | 14.13 | 3.30 | 1.98 | 1.85 | 72.13 | 18.63 | 4.49 | 2.25 | 2.11 | 68.03 | 21.53 | 5.02 | 1.98 | 2.51 | 30.52 | 27.48 | 20.08 | 9.25 | 5.28 |
| D | 79.04 | 14.62 | 2.72 | 1.81 | 1.81 | 68.95 | 22.77 | 3.75 | 1.94 | 2.20 | 62.23 | 27.17 | 5.30 | 2.46 | 2.20 | 14.23 | 29.88 | 27.81 | 13.97 | 6.34 |
| **Mean** | **75.61** | **19.62** | **2.11** | **1.23** | **1.29** | **66.97** | **25.48** | **4.26** | **1.50** | **1.38** | **60.84** | **29.45** | **5.86** | **1.57** | **1.68** | **21.62** | **31.34** | **23.68** | **10.57** | **5.19** |
| **Median** | **74.29** | **21.72** | **2.34** | **1.45** | **1.32** | **68.34** | **25.56** | **4.49** | **1.94** | **1.58** | **62.23** | **30.35** | **5.30** | **1.69** | **2.11** | **22.49** | **29.16** | **24.42** | **11.57** | **5.91** |
| **SD** | 3.14 | 4.76 | 1.00 | 0.72 | 0.68 | 4.25 | 3.98 | 1.87 | 0.81 | 0.78 | 6.20 | 4.28 | 2.37 | 0.83 | 0.91 | 9.09 | 5.35 | 7.27 | 3.74 | 1.54 |
| **SEM** | 1.19 | 1.80 | 0.38 | 0.27 | 0.26 | 1.61 | 1.50 | 0.71 | 0.31 | 0.30 | 2.34 | 1.62 | 0.90 | 0.32 | 0.34 | 3.44 | 2.02 | 2.75 | 1.41 | 0.58 |

*Cell figures represent % of sample intervals that individuals spent alone (0), with one (1), with two (2), with three (3) and with four (4) neighbours at each social distance category (C, P1, P2 and P3).

**Table 2.8** Scores of gregariousness of mandrills (% sample intervals)*

| | **Contact** | | | | | **P1** | | | | | **P2** | | | | | **P3** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Individual** | **0** | **1** | **2** | **3** | **4** | **0** | **1** | **2** | **3** | **4** | **0** | **1** | **2** | **3** | **4** | **0** | **1** | **2** | **3** | **4** |
| Z | 92.16 | 7.84 | 0.00 | 0.00 | 0.00 | 72.55 | 23.53 | 3.92 | 0.00 | 0.00 | 56.86 | 39.22 | 3.92 | 0.00 | 0.00 | 9.80 | 27.45 | 41.18 | 17.65 | 1.96 |
| N | 92.16 | 9.26 | 0.00 | 0.00 | 0.00 | 70.37 | 29.63 | 0.00 | 0.00 | 0.00 | 62.96 | 35.19 | 1.85 | 0.00 | 0.00 | 11.11 | 38.89 | 33.33 | 12.96 | 1.85 |
| NO | 92.16 | 5.45 | 0.00 | 0.00 | 0.00 | 94.55 | 5.45 | 0.00 | 0.00 | 0.00 | 89.09 | 10.91 | 0.00 | 0.00 | 0.00 | 47.27 | 29.09 | 16.36 | 7.27 | 0.00 |
| MA | 92.16 | 1.75 | 0.00 | 0.00 | 0.00 | 92.98 | 7.02 | 0.00 | 0.00 | 0.00 | 87.72 | 12.28 | 0.00 | 0.00 | 0.00 | 33.33 | 43.86 | 17.54 | 5.26 | 0.00 |
| OK | 92.16 | 3.77 | 0.00 | 0.00 | 0.00 | 94.34 | 5.66 | 0.00 | 0.00 | 0.00 | 90.57 | 9.43 | 0.00 | 0.00 | 0.00 | 37.74 | 37.74 | 18.87 | 5.66 | 0.00 |
| MP | 92.16 | 18.00 | 0.00 | 0.00 | 0.00 | 82.00 | 18.00 | 0.00 | 0.00 | 0.00 | 76.00 | 24.00 | 0.00 | 0.00 | 0.00 | 28.00 | 38.00 | 28.00 | 4.00 | 2.00 |
| AM | 92.16 | 13.21 | 0.00 | 0.00 | 0.00 | 77.36 | 18.87 | 0.00 | 0.00 | 0.00 | 69.81 | 30.19 | 0.00 | 0.00 | 0.00 | 16.98 | 45.28 | 28.30 | 7.55 | 1.89 |
| NI | 92.16 | 8.77 | 0.00 | 0.00 | 0.00 | 82.46 | 17.54 | 0.00 | 0.00 | 0.00 | 82.46 | 17.54 | 0.00 | 0.00 | 0.00 | 49.12 | 28.07 | 17.54 | 3.51 | 1.75 |
| NY | 92.16 | 4.00 | 0.00 | 0.00 | 0.00 | 70.00 | 8.00 | 0.00 | 0.00 | 0.00 | 88.00 | 12.00 | 0.00 | 0.00 | 0.00 | 38.00 | 38.00 | 20.00 | 4.00 | 0.00 |
| LK | 92.16 | 1.82 | 0.00 | 0.00 | 0.00 | 96.36 | 3.64 | 0.00 | 0.00 | 0.00 | 94.55 | 3.64 | 0.00 | 0.00 | 0.00 | 40.00 | 38.18 | 21.82 | 0.00 | 0.00 |
| CS | 92.16 | 12.28 | 0.00 | 0.00 | 0.00 | 82.46 | 17.54 | 0.00 | 0.00 | 0.00 | 80.70 | 19.30 | 0.00 | 0.00 | 0.00 | 52.63 | 28.07 | 17.54 | 1.75 | 0.00 |
| EB | 92.16 | 15.25 | 0.00 | 0.00 | 0.00 | 72.88 | 27.12 | 0.00 | 0.00 | 0.00 | 72.88 | 27.12 | 0.00 | 0.00 | 0.00 | 32.20 | 40.68 | 18.64 | 8.47 | 0.00 |
| MB | 94.74 | 5.26 | 0.00 | 0.00 | 0.00 | 92.98 | 7.02 | 0.00 | 0.00 | 0.00 | 91.23 | 8.77 | 0.00 | 0.00 | 0.00 | 19.30 | 35.09 | 31.58 | 7.02 | 7.02 |
| LE | 91.07 | 8.93 | 0.00 | 0.00 | 0.00 | 87.50 | 12.50 | 0.00 | 0.00 | 0.00 | 87.50 | 12.50 | 0.00 | 0.00 | 0.00 | 32.14 | 48.21 | 16.07 | 3.57 | 0.00 |
| NC | 90.74 | 9.26 | 0.00 | 0.00 | 0.00 | 79.63 | 20.37 | 0.00 | 0.00 | 0.00 | 74.07 | 25.93 | 0.00 | 0.00 | 0.00 | 31.48 | 33.33 | 22.22 | 9.26 | 1.85 |
| **Mean** | **92.16** | **8.32** | **0.00** | **0.00** | **0.00** | **83.23** | **14.79** | **0.26** | **0.00** | **0.00** | **80.29** | **19.20** | **0.38** | **0.00** | **0.00** | **31.94** | **36.66** | **23.27** | **6.53** | **1.22** |
| **Median** | **92.16** | **8.77** | **0.00** | **0.00** | **0.00** | **82.46** | **17.54** | **0.00** | **0.00** | **0.00** | **82.46** | **17.54** | **0.00** | **0.00** | **0.00** | **32.20** | **38.00** | **20.00** | **5.66** | **0.00** |
| **SD** | 0.84 | 4.83 | 0.00 | 0.00 | 0.00 | 9.43 | 8.40 | 1.01 | 0.00 | 0.00 | 11.17 | 10.59 | 1.09 | 0.00 | 0.00 | 13.14 | 6.50 | 7.52 | 4.44 | 1.86 |
| **SEM** | 0.22 | 1.25 | 0.00 | 0.00 | 0.00 | 2.43 | 2.17 | 0.26 | 0.00 | 0.00 | 2.89 | 2.73 | 0.28 | 0.00 | 0.00 | 3.39 | 1.68 | 1.94 | 1.15 | 0.48 |

*Scores are % of sample intervals that individuals spent alone (0), with one (1), with two (2), with three (3) and with four (4) neighbours at each social distance category (C, P1, P2 and P3).

Except at social distance $P_3$, mandrills scored higher than geladas in time spent alone ($p \leq 0.001$), and geladas scored higher than mandrills in time spent with just one neighbour [duos] and with two neighbours [trios] at C (geladas *versus* mandrills, duos: 19.6 *versus* 8.3%, respectively, $z = -3.7$, $p < 0.001$), at $P_1$ (geladas *versus* mandrills, duos: 25.5 *versus* 14.8%, respectively, $z = -2.7$, $p = 0.005$), and at $P_2$ (geladas *versus* mandrills, duos: 29.4 *versus* 19.2%, respectively, $z = -2.3$, $p = 0.021$). At $P_3$, there were no significant differences between the two species in any of the gregariousness measures (Tables 2.7-2.8; Fig. 2.6).

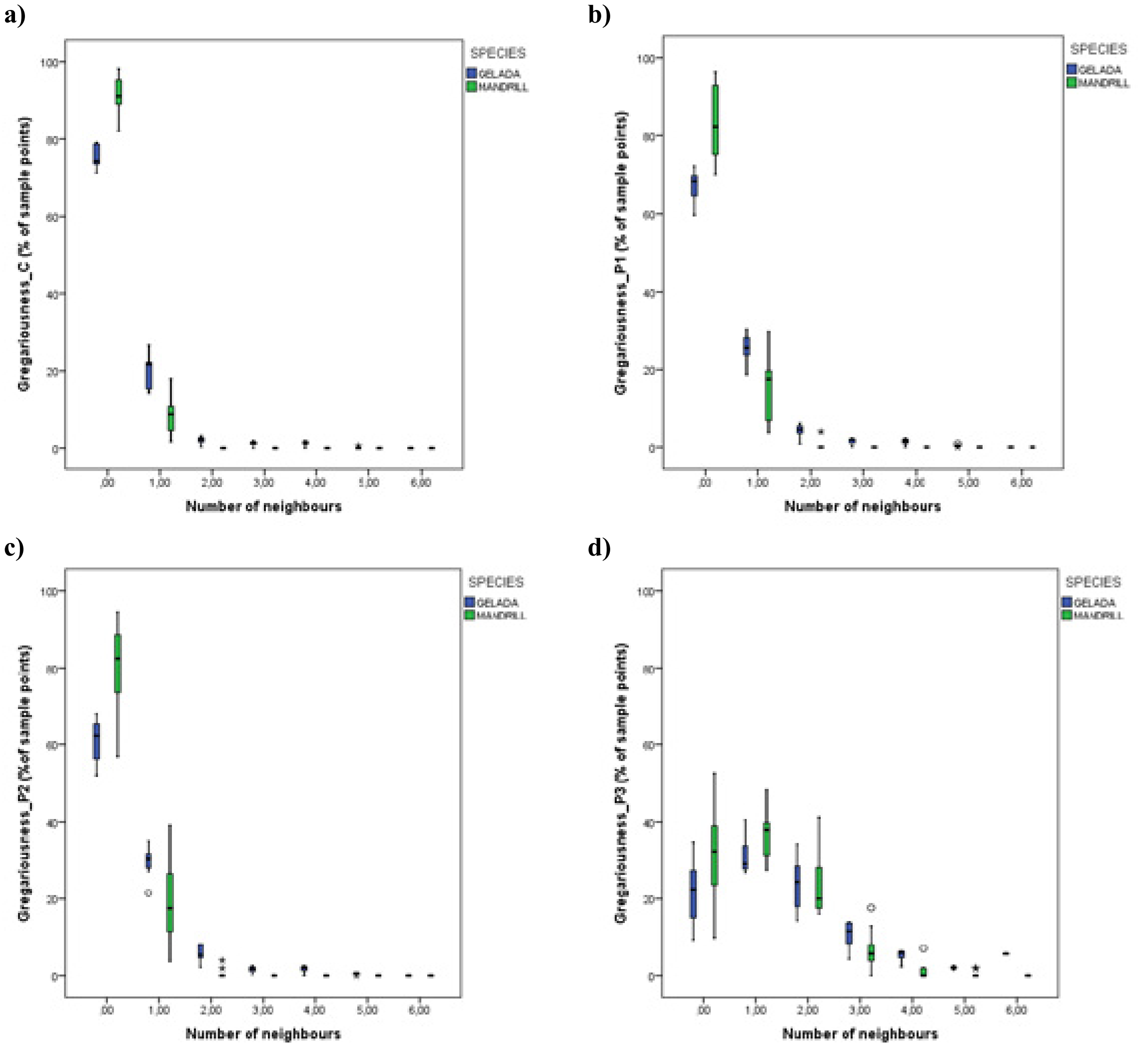


**Figure 2.6** Comparison of gregariousness in geladas *versus* mandrills, in the four distance categories: (a) contact [C], (b) within one arm's reach [$P_1$], (c) between one and two arms' reach [$P_2$], (d) between two arms and within four meters reach [$P_3$]. Number of neighbours: none (alone), 1 (duo), 2 (trio), 3 (quartet), etc. The box plots represent medians (black horizontal lines), interquartile range (boxes), minima and maxima (whiskers) as well as outliers (asterisks).

## Discussion

The analysis of the time that the individuals allocated to the four general behavioural activities, namely, *moving, foraging/feeding, resting* and *socializing*, showed that in spite of both groups being food-enhanced, the predominant activity was not socializing, which only accounted for 17.9% and 8.5% (geladas *versus* mandrills, respectively) of their total time budget. Instead, geladas' predominant activity was *foraging/feeding* (55.6%), whereas mandrills spent about the same time *resting* and *foraging/feeding* (33.8% and 33.5%, respectively). Furthermore, mandrills spent more time *moving* than *socializing* (15.5% *versus* 8.5%, respectively). Overall, compared to the mandrills, the geladas were more sociable (i.e., more often engaged in social interactions) and less inactive (i.e., resting).

In a detailed analysis of time budgets from three wild populations of geladas, Dunbar (1992a) reported that in all the three the greatest time was allocated to *feeding* 47.7% (range: 35.7-62.3%); as for the other three behavioural activities, no general pattern was found, though. *Moving* accounted for 17.5% (14.7-20.4%) of the total time budget, *resting* for 15.1% (5.2-26.3%), and *socializing* for 18.3% (16.0-20.5%). These figures obtained in wild populations match very closely the ones recorded in our gelada group, except moving (17.5% in Dunbar's study *versus* 7.5% in our study). In another more comprehensive analysis of time budgets in 18 wild populations of baboons (*Papio* and *Theropithecus*), Dunbar (1992b) reported the following time budgets: 31.85% (range: 20.3-59.3%) in *feeding*, 36.9% (range: 9.1-33.1%) in *moving*, 20.70% (range: 5.9-61.4) in *resting*, and 11.91% (range: 5.9-22.7%) in *socializing*. Again, the figures obtained in our study both in the gelada and mandrill groups fall well within the range of variation reported in Dunbar's (1992b) analysis of interpopulational differences in the time budgeting decisions of wild baboons.

When *Papio* baboons are partly food-provisioned in the wild, their time budgets change substantially compared to those of wild-feeding groups. Altmann and Muruthi (1988) found that a group (called Lodge Group) that fed on a garbage dump dropped its *feeding* time from 60% to 20%, and increased its *resting* time from 10% to 60%. In a 10-year longitudinal study of intrapopulational (as opposed to interpopulational) variation in the time budgets of three free-ranging groups of yellow baboons (*Papio cynocephalus*) in Amboseli, Kenya, Bronikowski and Altmann (1996) reported that under food-enhanced conditions baboons responded by increasing resting time rather than social time. Thus, they found that the partially food-enhanced Lodge Group spent less time *foraging*, much more time *resting*, and slightly more time *socializing* than two fully wild-feeding groups (*foraging*: 43% *versus* 69.8 and 75.2%; *resting*: 43.8 *versus* 21.5 and 16.4%; *socializing*: 13.3 *versus* 9.3 and 8.6%, respectively). That is, under relaxed ecological conditions (access to a human-derived food source), Lodge Group baboons increased *resting*, rather than *social time*. In our study, however, the geladas did not change substantially their *social time* or their *resting time*, either, even though they decreased their *foraging time*. The mandrill group, in contrast, exhibited much higher levels of *resting time* than *social time* under the ecologically relaxed conditions of captivity.

Our analyses of the time invested in each of the three main categories of social behaviour, namely, *affiliation (grooming)*, *aggression*, and *social play*, showed that affiliative behaviour was by far the social activity most common and play was next (*affiliation*: 87.4% and 94.4%; *play*: 11.6% and 4.3%, geladas *versus* mandrills, respectively). And interestingly, *aggression* was very infrequent (1% and 1.3%, respectively). Although one of the inevitable tolls of group-living is the increase of aggressive competition between group members (Dunbar, 1988; van Schaik, 1989), some researchers have underscored the fact that *aggressive behaviour* actually accounts for less than 1% of the primates' time budgets (Sussman *et al.,* 2003). Nevertheless, the variation in *social time* across different species of Old World primates is huge (8.6% ± 6.8%; Sussman and Garber, 2011), of which 89.9% is spent in affiliative behaviour. Once more again, these figures match closely the time allocated to these social categories in our two study groups of geladas and mandrills (*social time*: 17.9% and 8.5%, respectively; *affiliation*: 87.4% and 94.4%, respectively).

Variation in time budgets has also been analysed in a few studies of geladas and other Old World monkeys in captivity. In Bernstein's (1975) captive study of a large group of geladas, carried out over a 6-year period, he reported mean daily scores of 28% of time for *travelling*, 21% for *feeding*, 14% for *resting*, and 25% for other individual activities, which included self-directed and object manipulation actions. As for social behaviours, Bernstein (*ibidem*) reported that geladas spent a mean daily score of 28% of time in contact with one another (passive social time), and 25% of time engaged in grooming (active social time). In another gelada study by Filipcik *et al.* (2014), also carried out in a captive setting, the authors reported that individuals spent 44.1% of the time *foraging*/*feeding*, 24.6% *grooming*, 8.1% *moving*, and 7.7% *resting*. These figures compare well with those reported in the present study. Again no comparable data are available for mandrills.

In a study of the activity budgets of three captive groups of Japanese macaques (*Macaca fuscata*) housed in outdoor enclosures, two non-vegetated and one vegetated (although the enclosures also varied in several other physical and social conditions, for example, in spatial and social density), Jaman and Huffman (2008) reported that in all three groups, *resting* was the activity they spent in the longest; and both *resting* and *moving* were more prevalent in the non-vegetated enclosures than in the vegetated setting (45% *versus* 34.9%), whereas *feeding* and *grooming* times were longer in the vegetated than the nonvegetated groups (27.1% *versus* 14.2 and 16.1% *versus* 13.2, respectively). Jaman and Huffman (2013) compared time budgets in two groups of rhesus monkeys (*Macaca mulatta*) that were exposed to different levels of commensalism. The urban group was food-provisioned, whereas the rural group was not; the latter fed on natural vegetation as well as crops and food stolen from houses and shops. Compared to the urban, food-provisioned group, the rural group spent more time *feeding* (36.2% *versus* 22.4%) and *moving* (11% *versus* 10.8%), and less time *resting* (36.8% *versus* 46.1%) and *grooming* (11% *versus* 16.5%).

Our analysis of socio-spatial behaviour focused on two measures proposed in this study, namely, *sociality* and *gregariousness*, which were assessed at four distances, from contact (the most intimate circle around the individual) up to a circle that was between 2 arms' reach and within 4 meters. These increasing distances can be represented as discs with increasing radius (Fig. 2.2). The findings were important in several ways. Geladas and mandrills exhibited a closely similar overall *pattern* of *sociality*, but at the same time they significantly differed in their *overall sociality* assessed at most social distances. Thus, their sociality did not reach a cut-off point > 50% of time accompanied until the farthest distance was assessed ($P_3$: between 2 arms' reach and within 4 meters). However, in all three closer distances, i.e., C, $P_1$ and $P_2$, where the time spent accompanied was < 50%, geladas scored higher than mandrills.

The findings on gregariousness were even more remarkable. Again, geladas and mandrills were alike in their *pattern* of *gregariousness*, but differed in their *overall gregariousness*. At the first three social distance categories, they were significantly more likely to be alone than in company of just one neighbour (i.e., form duos). And, at the most distant category, $P_3$, they were significantly more likely to form trios than quartets. In other words, in both species, when not alone, the individuals spent most of the time in pairs or, at the farthest distance, in trios. On the other hand, at the first three distance categories, geladas were more gregarious than mandrills. Unfortunately, studies on nonhuman primate 'proxemics', i.e., patterns of proximity, are really scarce. There are just a few published studies on socio-spatial behaviour, however, the objectives, methods and measures that have been used are hugely diverse so that meaningful comparisons of results across studies are difficult to make (e.g., Fairbanks, 1976; Ehardt-Seward and Bramblett, 1980; Hornshaw, 1984; Corradino, 1990; Cowlishaw, 1999).

Although the time budgets recorded in the geladas and mandrills from the present study fell well within the range of variation reported in wild populations of *Theropithecus* and *Papio* baboons (Dunbar, 1992a, 1992b; Altmann and Muruthi, 1988; Bronikowski and Altmann, 1996), however, the former responded differently to the identically benign ecological conditions they faced in their captive settings. Although they both were food-provisioned and the enclosure they were free to wander around was densely vegetated, the geladas were found to keep a time budget profile closely similar to that reported in wild populations of baboons, except by a drop observed in moving time. This included a high level of foraging activity, a response typical of energy maximizers (van Doorn *et al.*, 2009). In contrast, the mandrills exhibited a relatively high investment in resting and foraging times, and a relatively reduced budget allocated to social time. The similarity between the activity time budgets of the two study groups and those reported for wild populations, including the relatively negligible amount of time engaged in aggressive interactions, challenges some myths about the impact of captive settings on the behaviours of primates. Some of these myths have been already debunked (de Waal, 1989; de Waal *et al.,* 2000; Judge, 2000; Colmenares, 2006), but many still need to be properly addressed.

Our findings on sociality and gregariousness also raise some key issues regarding the nature of the bonded sociality (group-living organization) of nonhuman primates. It is surprising, if not puzzling, that the study individuals spent so much time alone and, when accompanied, they tended to form small cliques made of just one or two neighbours. It seems as if groups, even in captivity, were actually made of aggregations of duos or trios.

Although the two study groups (a) were housed in similarly naturalized (vegetated and physically enriched) and sized (2,800-3,500 square meters) enclosures, (b) were exposed to identical local weather conditions, and (c) were food-provisioned and predation free, however, they were found to differ in time budgets and in sociality and gregariousness. Although one might be tempted to suggest that these differences could then be species-specific, however, it appears to us that given the amount of intraspecific variation reported in the social systems of primates and the fact that these two groups also differed in group size (social density) it would be more cautious to state that currently we cannot tell what key factors could account for such differences. We know, though, that the least socially dense group (i.e., the gelada group) was the most sociable and gregarious.

# CHAPTER 3

# Dominance gradient, reciprocity and interchange of aggression, grooming and punishment in geladas (*Theropithecus gelada*) and mandrills (*Mandrillus sphinx*): A comparative test of biological market predictions

**Abstract.** Primate sociality is typically bonded and bonds need to be serviced if they are to enhance the individuals' welfare and fitness. This bonded sociality of primate groups is the outcome of cooperative and competitive relationships between group members. Cooperative partnerships are sustained through the exchange of various kinds of behaviours over time, so establishing the nature of such exchanges and its underlying processes is paramount to an understanding of the evolution of cooperation. The Biological Market Theory has proposed that a group's dominance gradient should shape the supply and demand of services in the group (biological market) and this should in turn shape the patterns of exchange of such services among group members. The present comparative and correlational study draws on data of aggression, grooming, and punishment collected over a 22 week period in a group of geladas and a group of mandrills that varied in the steepness of their dominance hierarchies to test a number of assumptions and predictions of the biological market theory, particularly, the expected effect of the steepness of a group's dominance hierarchy on patterns of reciprocity (which should decline) and interchange (which should increase), assessed at group-level. The findings generally supported the predictions; however, grooming reciprocity was found to be unrelated to the dominance gradient, and although there was a negative association between grooming and punishment in the group with greater power differentials, the pattern was only marginally significant. The results highlight the importance of reciprocity and interchange in the servicing of bonds, its sensitivity to variations in the biological market, and the crucial role of partner choice in the evolution of cooperation and competition as key components of the bonded sociality of primates.

**Key words**: dominance gradient, reciprocity, interchange, aggression, grooming, punishment, biological market, *Theropithecus gelada, Mandrillus sphinx*

## Introduction

In many primate (and other mammalian) taxa group-living entails forming and maintaining long-term, highly individualized bonds with a set of group members. There is growing evidence that the quality of these social bonds crucially impacts the individuals' emotional well-being and physical health and, ultimately, their biological fitness (Dunbar and Shultz, 2010; Seyfarth and Cheney, 2012; Silk, 2007a, 2012). So, understanding the nature of such social bonds in terms of the behavioural, emotional, and cognitive processes that sustain them and how they contribute to shape a group's social structure and coherence, as well as its effects on the individuals' fitness is clearly needed (Dunbar and Shultz, 2010; Silk, 2012).

Bonds or social relationships between group members are typically assessed by analysing the behavioural actions that they exchange with one another over a given timespan in terms of 'who does what to whom, how often, and under what circumstances' (Mason, 1976; Seyfarth, Cheney and Hinde, 1978). These interactions can include, for example, the time engaged in passive physical contact or mere social proximity, the time engaged in and rates of grooming, and the rates of a number of other affiliative behaviours and of agonistic exchanges between dyads of individuals in the group. The analysis of characteristics such as, for example, the content, the frequency and the patterning of observable interactions between group members (i.e., what they do together, how often they do it, and how their interactions are organized over time, respectively) can then be used to abstract properties at the level of social relationships and of group structure (Hinde, 1976, 1983). For example, social relationships within dyads can be labelled asymmetrical *versus* symmetrical depending on whether the exchange of a given behaviour (or set of behaviours) between the incumbent partners is unidirectional or reciprocal, respectively. The behaviours that are typically exchanged mostly in one direction and that are associated with winning or losing access to contested resources have traditionally be used to assess the dominance status (or priority of access to desirable resources) of each individual in their *dyadic relationships* with others (Rowell, 1974; Bernstein, 1981; Drews, 1993). In many cases, an individual's dominance status in a dyadic relationship turns out to also be a good predictor of the frequency and direction of various behaviours, not just agonistic or competitive in kind, across multiple contexts. de Waal and Luttrell (1989; see also Flack and de Waal, 2004) and Thierry (2000, 2004) have used the label *dominance (or social) style* in this latter sense, that is, when a number of behavioural measures, including those related to dominance and competition over resources, tend to be inter-correlated (see chapter 4). Of course, if the dominance style of all or most dyads in a group (or even a species) falls within a given category, for example, despotic (strongly unidirectional) *versus* egalitarian (rather reciprocal), these labels can then be applied to describe group-level characteristics (de Waal and Luttrell, 1989; Flack and de Waal, 2004; Hand, 1986; Thierry, 2000, 2004).

In addition, some other labels have been (and can only be) used to describe properties of groups, for example, the *linearity* and the *steepness* of a group's *dominance hierarchy*. The former refers to the number of dominance relationships in the group that are transitive (non-circular), that is, for every, say, three individuals A, B, and C in a group the following holds: if A dominates B and B dominates C then A also dominates C (de Vries, 1998). The latter refers to the power differentials between adjacently ranked individuals; the hierarchy is said to be steep *versus* shallow depending on the magnitude of this power differential, respectively (de Vries, Stevens, and Vervaecke, 2006; Barrett and Henzi, 2001). Another term for designating the steepness of a hierarchy is *dominance gradient* (Barrett and Henzi, 2001, 2006; Balasubramaniam *et al.,* 2012).

*Sociality* is generally regarded as a cooperative arrangement where group members manage to access and enjoy a variety of valuable goods (e.g., greater safety from predators or success in inter-group competition for feeding sites) as a consequence of the collective, even if uneven, contribution of everyone in the group, for example, by detecting predators or monopolizing resources more effectively or by keeping higher levels of group cohesion via servicing social bonds and mending social conflicts (Aureli and Schaffner, 2006; Dunbar and Shultz, 2010; Majolo, Vizioli and Schino, 2008; van Hooff, 2001). If the bonded sociality of primate groups rests heavily on the cooperative efforts of their group members and on how they mitigate the potentially socially disruptive effects of intra-group aggression triggered by competition, then their social interactions should reflect the strategies of cooperation and competition the individuals play out to maximize their welfare and fitness (Kummer, 1978; Dunbar, 1984, 1988; Cords, 1997; Clutton-Brock, 2009; Silk, 2007a, 2007b; Majolo *et al.,* 2008; van Hooff and van Schaik, 1992).

Group members can thus be seen as 'social resources' potentially capable of providing 'services' that increase their partners' welfare and fitness, for example, companionship, grooming, help in fights, or punishment of norm transgressors. Of course, individuals vary widely in their value as social resources, for example, they typically vary in their ability and willingness to provide such limited and costly services and in their accessibility or availability due to competition with rivals pursuing similar goals (Colmenares, Zaragoza, and Hernández-Lloreda, 2002). In this context, then, individuals are expected to invest in and service bonds with valuable group members and to compete for and protect such partnerships whenever they are disrupted by intra-dyadic conflicts or are threatened by conflicts with third-parties (Kummer *et al.,* 1974; Kummer, 1975). One way of studying the nature of bonded sociality is by treating some social behaviours as 'investments' that individuals make to service their social bonds (Kummer, 1978; Dunbar, 1988; Cords, 1997) and by analysing whether or not they are reciprocally and contingently exchanged. The issue of contingent reciprocity is central to theories on the evolution of cooperative partnerships between unrelated individuals ever since Trivers proposed his highly influential theory of reciprocal altruism (Trivers, 1971, 2006). The issue remains controversial, though, with regard to how it is more appropriately theoretically modelled (i.e., partner control *versus* partner choice), how strong is the available correlational and empirical evidence for contingent reciprocity in animals, and what proximate mechanisms are claimed to be required to drive it (Aureli and Schaffner, 2006; Barrett and Henzi, 2006; Campenni and Schino. 2014; Cheney *et al.,* 2012; Clutton-Brock, 2009; de Waal and Brosnan, 2006; de Waal and Suchak, 2010; Hammerstein, 2003; Hammerstein and Noë, 2016; Hauser, McAuliffe and Blake, 2009; Hemelrijk, 1996, 2005, 2013; Jaeggi *et al.,* 2013; Noë, 2006a, 2006b; Schino and Aureli, 2009, 2010, 2016; Silk, 2007c; Stevens, Cushman and Hauser, 2005).

Sociality, at least of the bonded type so characteristic of many primate species, entails assemblies of individuals who recognize one another well, who interact repeatedly with one another over variable (sometimes lifelong) timespans and, importantly, who make, service, and terminate bonds with multiple group members simultaneously and serially. And there is a theoretical perspective, called the Biological Market Theory (BMT), which has capitalized on these (and other) key properties of bonded sociality (Noë and Hammerstein, 1994, 1995; Noë, 2001, 2006b; Hammerstein and Noë, 2016). The BMT is claimed to provide a more realistic account of the evolution of cooperation and reciprocity among unrelated individuals in group-living species than the traditional reciprocal altruism model based on variations of the two-player iterated prisoner's dilemma game proposed by Trivers (1971) and generally adopted by many subsequent researchers over the immediate two decades that followed his landmark paper. According to the BMT, group members are seen as 'traders' that exchange behaviours, called 'services', 'goods' or 'commodities', whose value is variable (context dependent) and is set by the law of supply and demand. Therefore, trading partners vary in their value or attractiveness as a function of the supply/demand ratio of the commodities they can provide. Two additional key characteristics of BMT, largely neglected in the traditional reciprocal altruism paradigm, are that cheating is controlled by switching partners (partner choice) rather than by punishing non-cooperating partners (partner control), and that traders belonging to a similar class compete with one another to be chosen by members of the other trading classes (i.e., outbidding competition).

The goal of the present study was to test a set of predictions that follow from a biological market approach to sociality and prosociality. Specifically, we were interested in studying the relation between the steepness of a group's dominance hierarchy and the patterns of reciprocity and interchange observed between aggression, grooming, and punishment. All the analyses were run at a group-level, that is, by correlating actor matrices with receiver matrices (Hemelrijk, 1990a, 1990b). Influenced by Seyfarth's early model of grooming distribution among female primates (Seyfarth, 1977, 1980), empirical studies of reciprocity and interchange have mostly focused on two behaviours, grooming and help (support) in fights, or some proxy for support, for example, attention to a partner's tape-recorded recruitment calls (Cheney *et al.,* 2012; Seyfarth and Cheney, 1984), although some studies have expanded it to include tolerance around food or other valuable resources (see Barrett and Henzi, 2006; de Waal and Brosnan, 2006; Silk, 2007c, for reviews). Here we expanded this traditional approach in various ways.

First, we examined **(a)** if the two study groups differed in one key property of their group structure, namely, the steepness of their groups' dominance hierarchy. Second, we assessed the relation between dominance rank and the rate of aggression, grooming, and punishment, and predicted **(b)** that this relation would be stronger where the dominance hierarchy is steeper. Third, we looked to see **(c)** if the rates of aggression, grooming, and punishment between individuals were positively related to the amount of time they spent together, within a relatively close social distance from one another. Four, we tested the assumption that a group's dominance gradient influences the relation between aggression given and received. We predicted **(d)** that the exchange of aggression should be more unidirectional (non-reciprocal) in the group with a steeper dominance hierarchy (Barrett, Gaynor, and Henzi, 2002; see also Barrett and Henzi, 2001, 2006). Five, we tested for reciprocity in grooming and predicted **(e)** that individuals would be more likely to reciprocate grooming in the group with a shallower dominance hierarchy. This is expected to be so because in such groups, where aggressive competition is relatively low, grooming cannot be traded for any valuable commodity other than grooming itself (Barrett and Henzi, 2001, 2006). Six, we studied the punisher-target dyad, rather than the supporter-supported dyad. Thus, in the present study, the actor-receiver matrices consisted of scores of *punishment given* and targeted aggression or *punishment received* (see de Waal and Luttrell, 1988, de Waal and Brosnan, 2006; Hemelrijk and Ek, 1991; Hemelrijk and Puga-Gonzalez, 2012). Moreover, we made two different punisher-target matrices, one for targets who were aggressors (*aggressor punishment*) and another for targets who were victims (*victim punishment*) in the initial aggressive encounter. We then predicted **(f)** that giving punishment to individuals who are victims in an aggressive interaction and receiving punishment as a victim were likely to exhibit a unidirectional pattern as, we assumed, interveners are likely to be relatively high-rankers and victims are likely to be relatively low-ranking individuals (see Hemelrijk and Puga-Gonzalez, 2012). We also predicted **(g)** that giving punishment to aggressors was less likely to be unidirectional as, we assumed, the power differential in punisher-aggressor dyads would be less marked than that in punisher-victim dyads. We further predicted **(h)** that this variation in the unidirectionality of victim-punishment (prediction *f*) and aggressor-punishment (prediction *g*) would be positively related to the dominance gradient of the group, that is, it should be more pronounced in the group with a steeper hierarchy. Seven, we examined **(i)** whether there was interchange of aggression for grooming. Here we did not spell out any prediction because the relation between these two behaviours could be positive, for example, if grooming was used to appease aggressors, or negative if aggression was used against uninvolved individuals, for example, as forms of side-directed or redirected aggression (see chapter 4). Eight, we studied whether aggression was interchanged for punishment, that is, for example, if individuals tended to direct aggression relatively more often toward those from whom they received relatively more frequently punishment (in aggressive interventions). We predicted **(j)** that this pattern of ‘counter-punishment’ would be less likely when the targets were victims (see above, predictions *f* and *g*) and when the dominance hierarchy was steeper (see above, prediction *h*). Finally, we assessed **(k)** the relation between grooming and punishment. Here we did not make any prediction for quite the same reasons we did not either in the study of the interchange of aggression for grooming (see above, prediction *i*).

## Material and Methods

### *Study groups and housing*

The present study was conducted from October 2010 until April 2011 at La Vallée des Singes, a large monkey and ape park located in Romagne (France). Subjects were the members of two groups of cercopithecoid African papionins, *Theropithecus gelada* and *Mandrillus sphinx* (Table 3.1), housed in roughly similar naturalistic settings in captivity.

**Table 3.1** Subjects of Study*

| **Individual**[1] | **Species** | **Sex** | **Age Class**[2] | **Observations** |
|---|---|---|---|---|
| Bongo (B) | Gelada | M | Adult (7) | Alpha male. Father of Saala, Dashan, Lengay and Haile |
| Lena (L) | Gelada | F | Adult (12) | Alpha female. Mother of Axoun, Saala and Lengay |
| Axoun (AX) | Gelada | M | Subadult (5) | |
| Saala (S) | Gelada | F | Juvenile (3) | |
| Ute (U) | Gelada | F | Adult (11) | Mother of Okoume, Dashan and Haile |
| Okoume (OK) | Gelada | M | Subadult (5) | |
| Dashan (D) | Gelada | M | Juvenile (3) | |
| Haile (H) | Gelada | F | Yearling (1) | |
| Lengay (LG) | Gelada | M | Infant (0.4) | |
| Zoulou (Z) | Mandrill | M | Adult (17) | Alpha male. Father of Amala, Mpassa, Mambassa, Okandja, Nouanda, Nyombé, Lekedi, Mboko, Ebaka, Leny, Natiwe and Mkoa |
| Nina (N) | Mandrill | F | Adult (16) | Alpha female. Mother of Amala, Mpassa, Mambassa, Okandja and Nouanda |
| Nouanda (NO) | Mandrill | F | Adult (9) | |
| Mambassa (MA) | Mandrill | F | Adult (7) | |
| Okandja (OK) | Mandrill | M | Subadult (6) | |
| Mpassa (MP) | Mandrill | F | Adult (5) | |
| Amala (AM) | Mandrill | F | Subadult (4) | |
| Nicky (NI) | Mandrill | F | Adult (14) | Mother of Nyombe, Lekedi and Natiwe |
| Nyombe (NY) | Mandrill | F | Adult (9) | |
| Lekedi (LK) | Mandrill | M | Subadult (6) | |
| Csilla (CS) | Mandrill | F | Adult (14) | Mother of Mboko, Ebaka, Leny and Mkoa |
| Ebaka (EB) | Mandrill | F | Adult (9) | |
| Mboko (MB) | Mandrill | M | Subadult (8) | |
| Leny (LE) | Mandrill | F | Subadult (4) | |
| Nico (NC) | Mandrill | M | Adult (12) | |
| Natiwe (NAT) | Mandrill | F | Infant (1) | |
| Mkoa (MK) | Mandrill | F | Infant (1) | |

*Sources: Charpentier *et al.* (2004); Dunbar (1980); Dunbar & Dunbar (1975); Kawai *et al.* (1983); Laidre & Yorzinski (2005); Leone & Palagi (2010).

[1] Code name in parentheses

[2] Years of age in parentheses

The group of geladas was made up of 9 individuals: one adult male, two adult females, two subadult males, one juvenile male, one juvenile female, one yearling female and one infant male. The group of mandrills comprised 17 individuals: two adult males, eight adult females, three subadult males, two subadult females, and two infant females. The two groups' enclosures consisted of an indoor facility, not visible to visitors, and a large outdoor compound (see Figure 2.1 in chapter 2). They included live and dead trees, big rocks, dens, wooden structures built with trunks placed in different positions and interconnected at different levels. The geladas' indoor area was divided into five interconnected rooms, 5.30m x 5.80m each. It was connected through a hatch system, which was always opened during the periods of data collection, to a 2,800m$^2$ outdoor exhibit surrounded by a water moat and visible to visitors. This open-air outdoor compound, which circled the indoor zone, had predominantly herbaceous vegetation with several trees and a wooden structure 4 meters high and 15 meters long. The mandrills' indoor area was also divided into five inter-connected rooms, 16.80m x 12.10m each with several wooden structures. It was connected through a hatch system, also opened during the sessions of data collection, to a 3,500m$^2$ outdoor exhibit, visible to visitors and surrounded by a water moat and the indoor area. This open-air outdoor area was densely vegetated (shrubs and trees) and included wooden structures and platforms above the ground.

In addition to the vegetation available in the enclosures that the individuals of both groups could and did consume *ad libitum*, geladas were fed four times per day (8.45 a.m., 11.45 a.m., 2.30 p.m. and 4 p.m.), and their diet included grass, vegetables, grains and pellets. Mandrills were fed six times per day (8.30 a.m., 12 a.m., 2.30 p.m., 3.30 p.m., 4.30 p.m. and 5.30p.m.); their diet included fruits, nuts, vegetables, grains and pellets. For both species water was always available *ad libitum*.

*Data collection: behavioural catalogue, and sampling and recording methods*

The ethograms used in this research were based on those used in previous studies of geladas (e.g., Dunbar and Dunbar, 1975; Leone and Palagi, 2010) and mandrills (e.g., Emory, 1975; Feistner, 1989; Mellen *et al.,* 1981). The categories of social *proximity* (i.e., social distance) were sampled via focal-group sampling in geladas and focal-animal sampling in mandrills, and were recorded via instantaneous (or point) sampling every 10 minutes; the observations were written down on pre-designed check sheets (Altmann, 1974; Hinde, 1973; Lehner, 1996; Martin & Bateson, 2007). To collect the other social behaviours we used two sampling methods concurrently, namely, focal-animal and focal-group sampling. Focal-animal follows were 10 min long. The behavioural observations were directly recorded on previously designed check sheets that contained 40 rows, each representing 15s time intervals, and 2 columns to write down focal-animal *versus* focal-group observations side by side, and the recording method was the continuous one (Altmann, 1974; Dunbar, 1976; Lehner, 1996; Martin and Bateson, 2007). All the records included information about the identity of the interacting individuals and their role (initiator, receiver, and third-party) in the interaction. In aggressive interactions, the initiator was labelled as aggressor (AG) and the target of the aggressor's behaviour as the victim (VT). An aggressive intervention was recorded when an initially uninvolved bystander or third-party directed aggressive behaviours towards the aggressor or the victim in an ongoing aggressive interaction. The period of data collection went on over 22 weeks, altogether, totalling 241 hours of focal-group sampling (geladas: 115 hours; mandrills: 126 hours). The study comprised 691 and 760 focal-individual samples of geladas and mandrills, respectively. We collected 261 instances of aggression in geladas and 1,389 in mandrills, 183 grooming episodes and 3,232 grooming intervals in geladas and 137 grooming episodes and 1,436 grooming intervals in mandrills, 90 aggressive interventions against aggressors (i.e., when third-parties punished the aggressor and, therefore, supported the victim) in geladas and 26 in mandrills, and 96 aggressive interventions against victims (i.e., when third-parties punished the victim and, therefore, supported the aggressor) in geladas and 244 in mandrills. In each group, individuals younger than 1.5 years of age were never sampled, so sample sizes were 7 for geladas and 15 for mandrills in the analyses.

### *Behavioural measures and data analyses*

The raw behavioural interactions recorded were aggregated into five conceptually and empirically based categories: proximity, dominance, aggression, affiliation (grooming), and punishment (third-party aggressive intervention targeting aggressors or victims). The category *proximity* included four different social distance measures, contact (physical contact), $P_1$ (within 1 arm's reach but not in contact), $P_2$ (within 2 arms' reach but more than 1 arm's reach away from the partner), and $P_3$ (within a distance greater than 2 arms' reach but less than 4m away from the partner). We constructed four proximity matrices where cell entries represented the percentage of time (15s intervals) that each individual spent within each proximity distance to each and every other group member. In chapter 2 these matrices were used to study the socio-spatial behaviour of the two groups. Here, however, the proximity matrices were used in partial rowwise matrix correlations to determine if the correlations between aggression, grooming and punishment were genuine or just by-products of their correlations with proximity measures. In this context, then, the proximity measures (i.e., time spent together at four different social distances) were used as symmetrical relationship characteristics (*sensu* de Waal and Luttrell, 1988; de Waal and Brosnan, 2006).

The category *dominance* included four (in mandrills) and five (in geladas) behavioural measures, namely, supplanting (without overt signals of aggression, in a competitive context), non-agonistic presenting, screaming in response to aggression, and avoid (move away from another in response to non-agonistic approach) in both species, and, in geladas, the extra measure bared teeth display (Leone and Palagi, 2010). An exploratory analysis revealed that they were all consistently unidirectional and intercorrelated and, more importantly, they have been conceptualised as formal indicators of dominance or subordinance status (de Waal and Luttrell, 1985; Flack and de Waal, 2004; see also Preuschoft, 1999). The early literature often referred to some of these dominance-related measures as approach-retreat patterns, specifically, supplanting and avoid (e.g., Richards, 1974; Rowell, 1974). The Spearman rank correlation between the aggregated hourly scores of (marginal totals for) giving and (marginal totals for) receiving these dominance-related behaviours was negative in both species (geladas: $r_s = -0.46$, N= 7; $0.10 < P < 0.20$, NS; mandrills: $r_s = -0.63$, N = 15, $p < 0.02$). The resulting individual x individual square dominance rank matrix was later used in two analyses. First, it was used to work out the linearity and the steepness of each group's dominance hierarchy. We assigned dominance ranks to the individuals in each group on the basis of the direction and frequency of dominance-related scores. From this we constructed a 'hypothesis matrix' in which entries were the ranks of the column individuals (Hemelrijk, 1990b; Mitani, 2006; Watts, 2000a, 2002). We followed the convention by assigning rank 1 to the alpha individual, rank 2 to the second-highest ranking, and so on. Second, we used the dominance rank matrix to determine if patterns of reciprocity or interchange held up after statistically controlling for dominance rank. The category *aggression* included several behavioural measures of noncontact aggression (e.g., threats, lunges) and of contact aggression (e.g., hits, pulls) which were also scored as hourly rates. Although we recorded several affiliative behaviours, our final category *affiliation* was actually based only on two separate measures of grooming: hourly rate of grooming episodes and % of time spent grooming. Finally, the category *punishment* was divided into two separate measures that were also scored as hourly rates: aggressor punishment (when the third-party intervened in an ongoing dyadic aggressive conflict by aggressively targeting the aggressor and, therefore, supporting the victim) and victim punishment (when the third-party aggressively targeted the victim and, therefore, supported the aggressor).

Exploratory analyses revealed the existence of statistically significant positive correlations between the scores recorded during focal-individual and focal-group sampling (mean Spearman Rank coefficient = 0.84, $P < 0.05$ in geladas and 0.76, $P < 0.002$ in mandrills), so both sources of data were summed for each individual and then corrected for the total observation time (focal-individual plus focal-group sampling time).

We ran several sets of analyses ($N = 7$ geladas and $N = 15$ mandrills). First, we used the Mann-Whitney two-independent samples test, U (Neave and Worthington, 1988; Siegel and Castellan, 1988; Zar, 1999) to compare the hourly rates of dominance-based behaviours, aggression-based behaviours, punishment of aggressors (i.e., 'aggressor punishment'), punishment of victims (i.e., 'victim punishment'), and grooming, and the percent of grooming time. Here, we used two-tailed probabilities and the level of significance was set at 5%. For this we used SPSS version 20. Second, we used the software package MatMan, version 1.1 (NOLDUS Information Technology, Wageningen, The Netherlands, 2003) to calculate Landau's *linearity* index, $h$, and the corrected version $h'$ for unknown relationships (de Vries, 1995). The statistical significance (p-value) of this index was based on 10,000 randomizations. To calculate the *steepness* of each group's dominance hierarchy we used the R package for dyadic data analysis (de Vries, Stevens, and Vervaecke, 2006; Leiva *et al.,* 2010). This index is based on normalized David's scores (de Vries *et al.,* 2006; Balasubramaniam *et al.,* 2012).

Within the actor-receiver model adopted in this paper (Hemelrijk, 1990b), we assessed 'relative' *reciprocity* (or bidirectionality) of aggression, grooming, and punishment, and *interchange* of aggression, grooming and punishment, that is, whether each individual gave only relatively more often to those from whom it received more frequently in return, the same behaviour (in reciprocity) or different behaviour (in interchange). This analysis is done on an ordinal scale and 'within' each individual. We run two types of rowwise matrix correlations of actor-receiver square matrices containing structural zeros in the diagonal (de Vries, 1993; Hemelrijk, 1990a, 1990b). First, we run bivariate rowwise correlations between five actor-receiver matrices and its corresponding transposed versions (i.e., aggression given and received, grooming rate given and received, grooming time given and received, aggressor punishment given and received and victim punishment given and received). We also run the same kind of rowwise correlations but now with different behaviour matrices, looking for patterns of interchange between different behaviours in both directions, that is, behaviour matrix X vs behaviour matrix Y transposed (e.g., grooming given *versus* punishment received) and vice versa, that is, behaviour matrix X transposed *versus* behaviour matrix Y (e.g., grooming received *versus* punishment given).

Second, we run partial rowwise matrix correlations (de Vries, 1993; Hemelrijk, 1990a) where we tried to determine if the correlation between two behaviour matrices, say X and Y, remained while statistically holding constant a third variable matrix Z that was itself correlated with X, Y, or both. If the correlation between two actor and receiver matrices (X and Y) reached a $P < 0.10$ and any of them was found to correlate ($P < 0.10$) with dominance rank or with any of the four proximity measures, we then explored if the correlation was genuine or a by-product of the correlation of each of them with the third matrix variable (Z). For all matrix correlations we used the MatMan statistical package. We used the $K_r$ test (i.e., the Kendall's statistic S is calculated for each pair of rows and summed over all rows). The probability of the observed value is calculated using Mantel's permutation method (Hemelrijk, 1990a, 1990b). In these analyses, rows and columns are permuted simultaneously. We used 10,000 permutations. In all these analyses the critical level of significance ($\alpha$) was one-tailed and set at $P < 0.05$.

## Results

### *Differences in aggression, grooming and punishment*

Mandrills outperformed geladas (M > G) in their rates of the aggregated categories labelled *dominance* and *aggression*, although the differences in the latter measure only approached statistical significance (U = 18, Z = -2.43, p = 0.01; U = 29, Z = -1.66, p = 0.10, NS; respectively; Fig. 3.1). In contrast, geladas outperformed mandrills (G > M) in the two affiliation-related *grooming* measures analysed (grooming time: U = 4, Z = -3.42, P < 0.001 and grooming rate: U = 19, Z = -2.37, P = 0.007, respectively; Fig. 3.2) and in the rate of *aggressor punishment* (U = 7, Z = -3.29, P = 0.001; Fig. 3.3). They did not differ in their rates of *victim punishment*, though (U = 51, Z = -0.11, P = 0.93, NS; Fig. 3.3).

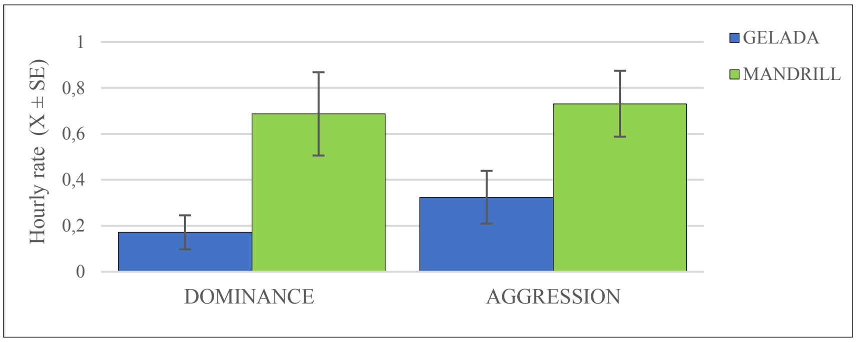


**Figure 3.1** Dominance- and aggression-based measures in geladas *versus* mandrills.

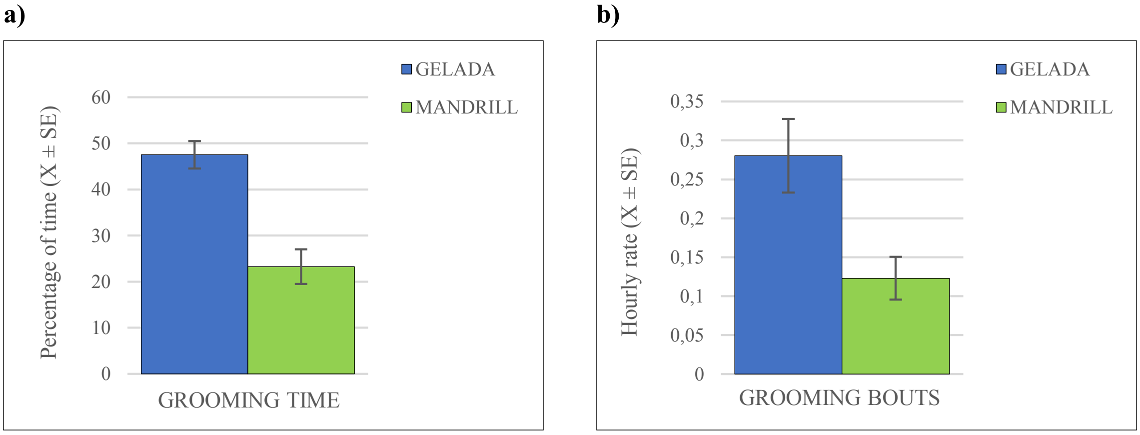


**Figure 3.2** Affiliation-related measures. a) Grooming time (%) and b) grooming bouts (rate) in geladas *versus* mandrills.

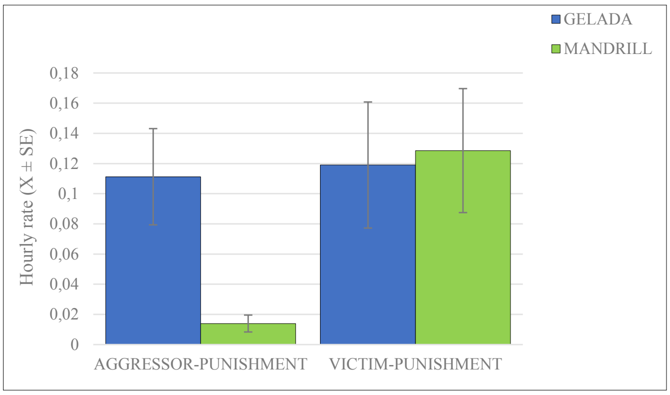


**Figure 3.3** Aggressor-Punishment and Victim-Punishment in geladas *versus* mandrills.

### *Linearity and Steepness of the dominance hierarchies*

The geladas' dominance hierarchy was highly linear (h' = 1, K = 1, $\chi 2 = 48$, df = 23.33, P = 0.0031), but shallow (steepness = 0.057, P = 1.0; Fig. 3.4). In contrast, the dominance hierarchy of mandrills was also linear (h' = 0.907, K = 0.907, $\chi 2 = 96.19$, df = 22.56, P = 0.00001), but highly steep (steepness = 0.74, P = 0.0001; Fig. 3.4).

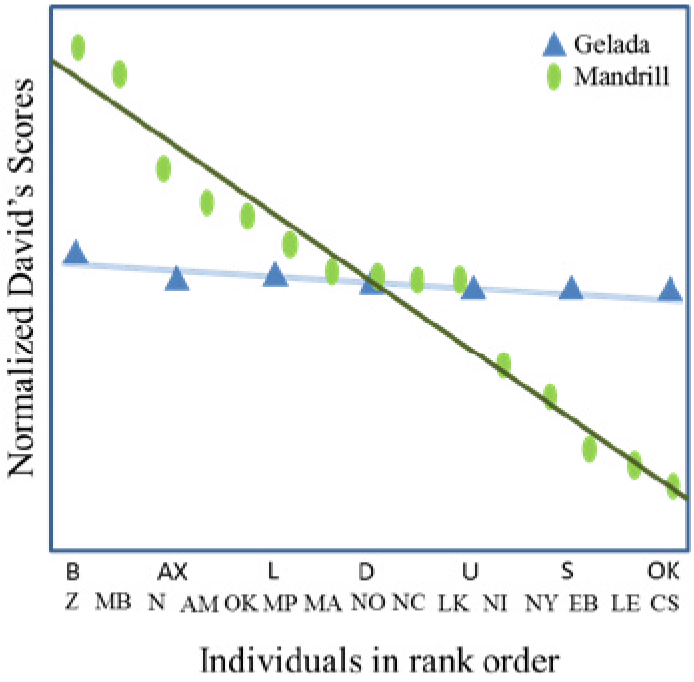


**Figure 3.4** Normalized David's scores plotted against the rank of 7 geladas (B–OK) and 15 mandrills (Z-CS), ranked from 1 (highest) to 7 or 15 (lowest), respectively. The straight lines fitted through the normalized David's scores are based on the dyadic dominance index (Dij). Geladas: $Y = -0.05739X + 3.23$; mandrills: $Y = -0.7414X + 12.93$.

### *Dominance Rank, Aggression, Grooming and Punishment*

Low-ranking individuals received relatively more aggression than high-ranked group members in both species ($K_r = 37$, $\tau_{Kr} = 0.3523$, P = 0.0075; $K_r = 359$, $\tau_{Kr} = 0.3124$, P = 0.0002), but in geladas only high-rankers gave relatively more aggression than low-rankers ($K_r = -55$, $\tau_{Kr} = -0.5288$, P = 0.0195, Table 3.2). Thus, relative to low-rankers, high-ranking individuals tended to receive less aggression (in both species) and to give more aggression (only in geladas). In geladas, but not in mandrills, high-ranking individuals received relatively more grooming, both in rate and time measures, than low rankers did; however, in neither case did the correlations reach statistical significance, although there was a marginal trend ($K_r = -20$, $\tau_{Kr} = -0.2104$, P = 0.0683 and $K_r = -16$, $\tau_{Kr} = -0.1531$, P = 0.0528; Table 3.2). In mandrills, high-ranking aggressors were relatively more often targets of third-parties' aggressive interventions than low-ranking aggressors were ($K_r = -43$, $\tau_{Kr} = -0.0934$, P = 0.0508; Table 3.2).

**Table 3.2** Results of matrix permutation tests of the association between dominance rank and the behaviours analysed*

| **Behaviour** | **Species** | **Kr** | $\tau_{Kr}$ | **P** |
|---|---|---|---|---|
| *Aggression given* | **G** | 37 | 0.3523 | **0.0075** |
| | **M** | 359 | 0.3124 | **0.0002** |
| *Aggression received* | **G** | -55 | -0.5288 | **0.0195** |
| | M | 9 | 0.01210 | 0.4485 |
| *Grooming (rate) given)* | **G** | -20 | -0.2104 | **0.0683** |
| | M | -7 | -0.0095 | 0.4402 |
| *Grooming (rate) received* | G | -11 | -0.1150 | 0.1930 |
| | M | 9 | 0.0121 | 0.4466 |
| *Grooming (time) given* | **G** | -16 | -0.1531 | **0.0528** |
| | M | 30 | 0.0288 | 0.3544 |
| *Grooming (time) received* | G | 0 | 0 | 0.5325 |
| | M | 21 | 0.0201 | 0.4182 |
| *Aggressor-Punishment given* | G | -28 | -0.3266 | 0.1130 |
| | **M** | -43 | -0.0934 | **0.0508** |
| *Aggressor-Punishment received* | **G** | -30 | -0.3718 | **0.0330** |
| | **M** | -98 | -0.2071 | **0.0025** |
| *Victim-Punishment given* | G | 13 | 0.1505 | 0.2208 |
| | **M** | 172 | 0.1903 | **0.0506** |
| *Victim-Punishment received* | **G** | -27 | -0.3219 | **0.0363** |
| | **M** | -295 | -0.3306 | **0.0001** |

**Kr* and Tau Kr ($\tau_{Kr}$) values give results of tests that examine the relative association between the dominance rank matrix and the actor and the receiver matrices for each of the behaviours analysed in this study. Geladas (G), N = 7 and mandrills (M), N = 15. P-values < 0.10 are shown in **boldface.**

However, also only in mandrills, the reversed pattern was found for victims that were targeted by aggressive interveners; here, high-ranking victims were relatively less often targets of punishment by third-party interveners ($K_r = 172$, $\tau_{Kr} = 0.1903$, $P = 0.0506$; Table 3.2). In both species, high-rankers were relatively more often than low-ranked individuals involved in punishing both aggressors (geladas, $K_r = -30$, $\tau_{Kr} = -0.3718$, $P = 0.033$; mandrills, $K_r = -98$, $\tau_{Kr} = -0.2071$, $P = 0.0025$) and victims (geladas, $K_r = -27$, $\tau_{Kr} = -0.3219$, $P = 0.0363$; mandrills, $K_r = -295$, $\tau_{Kr} = -0.3306$, $P = 0.0001$; Table 3.2).

### *Proximity, Aggression, Grooming and Punishment*

In both species, the four proximity measures analysed (i.e., C, $P_1$, $P_2$ and $P_3$) correlated positively with the four measures of grooming, that is, grooming rate given and received, and grooming time given and received (Table 3.3). There was also a positive correlation between aggression received and time spent at $P_2$ and at $P_3$ in mandrills (Table 3.3). In geladas there was no correlation between proximity, at any distance, and aggressor-punishment or victim-punishment, whereas in mandrills, aggressor-punishment given was positively associated with time spent at C, $P_1$, $P_2$ and $P_3$, aggressor-punishment received was positively associated with time spent at $P_2$ and $P_3$; and, finally, victim-punishment received was positively associated with time spent at $P_2$ (Table 3.3).

**Table 3.3** Results of matrix permutation tests of the association between proximity and the behaviours analysed*

| Behaviour | Species | Contact | | | Proximity 1 (< 1 arm's reach) | | | Proximity 2 (1-2 arms' reach) | | | Proximity 3 (2 arms' reach – 4 meters) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Kr | $\tau_{Kr}$ | P | Kr | $\tau_{Kr}$ | P | Kr | $\tau_{Kr}$ | P | Kr | $\tau_{Kr}$ | P |
| *Aggression given* | G | 15 | 0.1428 | 0.1669 | 22 | 0.2105 | **0.0773** | 23 | 0.2190 | **0.0646** | 31 | 0.2952 | **0.0186** |
| | M | 14 | 0.0184 | 0.3836 | -18 | -0.0247 | 0.3521 | -29 | -0.0458 | 0.2523 | -97 | -0.0847 | **0.0783** |
| *Aggression received* | G | 3 | 0.0288 | 0.4700 | 2 | 0.0193 | 0.4890 | 5 | 0.0480 | 0.4137 | 7 | 0.0673 | 0.3839 |
| | M | -20 | -0.0262 | 0.3322 | -7 | -0.0096 | 0.4434 | 80 | 0.1261 | **0.0421** | 172 | 0.1496 | **0.0090** |
| *Grooming (rate) given* | G | 40 | 0.4209 | **0.0140** | 38 | 0.4018 | **0.0123** | 34 | 0.3577 | **0.0262** | 38 | 0.3998 | **0.0124** |
| | M | 207 | 0.4284 | **0.0001** | 151 | 0.3271 | **0.0002** | 87 | 0.2164 | **0.0060** | 129 | 0.1771 | **0.0041** |
| *Grooming (rate) received* | G | 53 | 0.5545 | **0.0018** | 45 | 0.4730 | **0.0046** | 41 | 0.4289 | **0.0118** | 45 | 0.4708 | **0.0044** |
| | M | 209 | 0.4282 | **0.0001** | 156 | 0.3345 | **0.0001** | 104 | 0.2561 | **0.0027** | 105 | 0.1427 | **0.0207** |
| *Grooming (time) given* | G | 62 | 0.5933 | **0.0005** | 45 | 0.4326 | **0.0055** | 42 | 0.4019 | **0.0079** | 36 | 0.3445 | **0.0227** |
| | M | 325 | 0.4726 | **0.0001** | 202 | 0.3074 | **0.0003** | 85 | 0.1486 | **0.0355** | 196 | 0.1891 | **0.0027** |
| *Grooming (time) received* | G | 70 | 0.6698 | **0.0002** | 51 | 0.4903 | **0.0033** | 50 | 0.4784 | **0.0033** | 38 | 0.3636 | **0.0210** |
| | M | 320 | 0.4650 | **0.0001** | 227 | 0.3452 | **0.0001** | 95 | 0.1660 | **0.0227** | 166 | 0.1600 | **0.0104** |
| *Aggressor-Punishment given* | G | -2 | -0.0233 | 0.4721 | -12 | -0.1406 | 0.1938 | 2 | 0.0233 | 0.4693 | -12 | -0.1399 | 0.2347 |
| | M | 49 | 0.1610 | **0.0173** | 42 | 0.1445 | **0.0316** | 35 | 0.1383 | **0.0349** | 53 | 0.1156 | **0.0347** |
| *Aggressor-Punishment received* | G | -6 | -0.0743 | 0.3542 | -6 | -0.0747 | 0.3485 | -8 | -0.0991 | 0.3010 | -2 | -0.0247 | 0.4983 |
| | M | 26 | 0.0830 | 0.1307 | 35 | 0.1170 | **0.0681** | 45 | 0.1729 | **0.0249** | 78 | 0.1654 | **0.0047** |
| *Victim-Punishment given* | G | -17 | -0.1968 | 0.1044 | -19 | -0.2211 | **0.0665** | -13 | -0.1505 | 0.1852 | -15 | -0.1737 | 0.1425 |
| | M | -9 | -0.0150 | 0.4010 | -24 | -0.0420 | 0.2811 | -11 | -0.0221 | 0.4044 | -57 | -0.0633 | 0.1559 |
| *Victim-Punishment received* | G | -17 | -0.2026 | **0.0842** | -14 | -0.1677 | 0.1363 | -11 | -0.1311 | 0.2030 | -17 | -0.2026 | **0.0902** |
| | M | -5 | -0.0084 | 0.4433 | -10 | -0.0177 | 0.4020 | 78 | 0.1589 | **0.0172** | 72 | 0.0809 | **0.0926** |

**Kr* and Tau Kr ($\tau_{Kr}$) values give results of tests that examine the relative association between the four proximity matrices and the actor and the receiver matrices for each of the behaviours analysed in this study. Geladas (G), N = 7, and mandrills (M), N = 15. P-values < 0.10 are shown in **boldface.**

*Reciprocity of Aggression, Grooming and Punishment*

Aggression was unidirectional in mandrills ($K_r$ = -149, $\tau_{Kr}$ = -0.1535 P = 0.0124), although this negative association vanished when dominance rank was partialled out (Table 3.4). Nevertheless, this reciprocal pattern was independent of association time at $P_2$ and $P_3$ (see Table 3.5). There was reciprocity of grooming rate and time in both species (geladas, $K_r$ = 93, $\tau_{Kr}$ = 0.8416, P = 0.0001 and $K_r$ = 115, $\tau_{Kr}$ = 0.8214, P = 0.0001; mandrills, $K_r$ = 183, $\tau_{Kr}$ = 0.4633, P = 0.0001 and $K_r$ = 409, $\tau_{Kr}$ = 0.5160, P = 0.0001), a pattern that was independent of dominance rank and proximity in both species and measured both as rate and as percent of time (Tables 3.4 and 3.5). Aggressor-punishment was reciprocal in both species, although in mandrills only approached statistical significance (geladas, $K_r$ = 27, $\tau_{Kr}$ = 0.3179, P = 0.0196; mandrills, $K_r$ = 18, $\tau_{Kr}$ = 0.1128, P = 0.0783, NS; Table 3.4). In contrast, victim-punishment was unidirectional, but only in mandrills ($K_r$ = -113, $\tau_{Kr}$ = -0.1913, P = 0.0038; Table 3.4), a pattern that held up after controlling for rank and the four measures of proximity (Tables 3.4 and 3.5).

**Table 3.4** Results of Kr for reciprocity of aggression, grooming, and punishment*

| Reciprocity | Species | Kr | $\tau_{Kr}$ | P |
|---|---|---|---|---|
| Aggression | G | 11 | 0.0774 | 0.2705 |
| | **M** | -149 | -0.1535 | **0.0124** |
| *Controlled for Rank* | M | | -0.0529 | 0.2191 |
| Grooming (rate) | **G** | 93 | 0.8416 | **0.0001** |
| | **M** | 183 | 0.4633 | **0.0001** |
| *Controlled for Rank* | **G** | | 0.8203 | **0.0002** |
| | **M** | | 0.4634 | **0.0001** |
| Grooming (time) | **G** | 115 | 0.8214 | **0.0001** |
| | **M** | 409 | 0.5160 | **0.0001** |
| *Controlled for Rank* | **G** | | 0.8075 | **<0.001** |
| | **M** | | 0.5158 | **0.0001** |
| Aggressor-Punishment | **G** | 27 | 0.3179 | **0.0196** |
| | **M** | 18 | 0.1128 | **0.0783** |
| *Controlled for Rank* | G | | 0.1557 | 0.2023 |
| | M | | 0.0960 | 0.1049 |
| Victim-Punishment | G | 10 | 0.1136 | 0.2242 |
| | **M** | -113 | -0.1913 | **0.0038** |
| *Controlled for Rank* | **M** | | -0.1386 | **0.0356** |

**Kr* and Tau Kr ($\tau_{Kr}$) values give results of tests that examine the relative association between the actor and the receiver matrices, i.e., reciprocity, for each behaviour analysed. Whenever a reciprocity pattern was found (P < 0.10) and any of the behaviour matrices was found to correlate with dominance rank (see Table 3.2), we then ran partial rowwise correlations holding the dominance rank matrix controlled and give the partial Tau Kr. Geladas (G), N = 7 and mandrills (M), N = 15. P-values < 0.10 are shown in **boldface.**

**Table 3.5** Results of Kr for reciprocity of aggression, grooming, and punishment*

| **Reciprocity** | **Species** | **Kr** | $\tau_{Kr}$ | **P** |
|---|---|---|---|---|
| Aggression | G | 11 | 0.0774 | 0.2705 |
| | **M** | -149 | -0.1535 | **0.0124** |
| *Controlled for P2* | **M** | | -0.1490 | **0.0169** |
| *Controlled for P3* | **M** | | -0.1429 | **0.0193** |
| Grooming (rate) | **G** | 93 | 0.8416 | **0.0001** |
| | **M** | 183 | 0.4633 | **0.0001** |
| *Controlled for C* | **G** | | 0.7781 | **0.0003** |
| | **M** | | 0.3427 | **<0.001** |
| *Controlled for P1* | **G** | | 0.7818 | **0.0004** |
| | **M** | | 0.3973 | **<0.001** |
| *Controlled for P2* | **G** | | 0.7911 | **0.0005** |
| | **M** | | 0.4321 | **<0.001** |
| *Controlled for P3* | **G** | | 0.7822 | **0.0002** |
| | **M** | | 0.4496 | **<0.001** |
| Grooming (time) | **G** | 113 | 0.8214 | **0.0001** |
| | **M** | 409 | 0.5160 | **0.0001** |
| *Controlled for C* | **G** | | 0.6703 | **0.0003** |
| | **M** | | 0.3797 | **<0.001** |
| *Controlled for P1* | **G** | | 0.7456 | **0.0003** |
| | **M** | | 0.4590 | **0.0001** |
| *Controlled for P2* | **G** | | 0.7533 | **0.0001** |
| | **M** | | 0.5039 | **<0.001** |
| *Controlled for P3* | **G** | | 0.7693 | **0.0004** |
| | **M** | | 0.5012 | **<0.001** |
| Aggressor-Punishment | **G** | 27 | 0.3179 | **0.0196** |
| | **M** | 18 | 0.1128 | **0.0783** |
| *Controlled for C* | **G** | | 0.2570 | **0.0874** |
| | **M** | | 0.1011 | **0.0944** |
| *Controlled for P1* | **G** | | 0.2507 | **0.0965** |
| | M | | 0.0976 | 0.1088 |
| *Controlled for P2* | **G** | | 0.2617 | **0.0838** |
| | M | | 0.0912 | 0.1177 |
| *Controlled for P3* | **G** | | 0.2571 | **0.0872** |
| | M | | 0.0957 | 0.1074 |
| Victim-Punishment | G | 10 | 0.1136 | 0.2242 |
| | **M** | -113 | -0.1913 | **0.0038** |
| *Controlled for C* | **M** | | -0.1915 | **0.0049** |
| *Controlled for P1* | **M** | | -0.1923 | **0.0015** |
| *Controlled for P2* | **M** | | -0.1903 | **0.0039** |
| *Controlled for P3* | **M** | | -0.1872 | **0.0053** |

**Kr* and Tau Kr ($\tau_{Kr}$) values give results of tests that examine the relative association between the actor and the receiver matrices, i.e., reciprocity, for each behaviour analysed. Whenever a reciprocity pattern was found ($P < 0.10$) and any of the behaviour matrices was found to correlate with each of the four proximity matrices (see Table 3.3), we then ran partial rowwise correlations holding the proximity matrix controlled and give the partial Tau Kr. Geladas (G), N = 7 and mandrills (M), N = 15. P-values < 0.10 are shown in **boldface.**

### *Interchange of Aggression, Grooming, and Punishment*

Although in both species there was a trend ($0.05 < P < 0.10$) for the interchange of aggression given for grooming rate received, and of aggression received for grooming rate given, only in geladas and only in one of the directions, i.e., aggression received for grooming rate given, the correlation reached statistical significance ($K_r = 49$, $\tau_{Kr} = 0.3934$, $P = 0.0005$; Table 3.6). Nevertheless, this correlation was dependent of dominance rank (Table 3.6) and independent of proximity at any of the four social distances analysed (Table 3.7). The analysis of interchange of aggression and the other measure of grooming, i.e., percentage of time spent grooming, revealed that only in geladas the interchange was confirmed in both directions ($K_r = 33$, $\tau_{Kr} = 0.2332$, $P = 0.0299$; $K_r = 51$, $\tau_{Kr} = 0.3629$, $P = 0.0009$; Table 3.6), although, this correlation did no longer hold after controlling for dominance rank (Table 3.6), the four proximity measures in aggression given for grooming time received (Table 3.7), and the two distant proximity measures analysed, i.e., $P_2$ and $P_3$, in aggression received for grooming time given (Table 3.7). In geladas, there was interchange of aggression received for aggressor-punishment given ($K_r = 54$, $\tau_{Kr} = 0.4820$, $P = 0.0011$; Table 3.6); however, this correlation was not independent of rank (Table 3.6), although it was independent of any of the four proximity measures (Table 3.7). In mandrills, there was a significant, but negative, association between aggression and victim-punishment, in both directions ($K_r = -153$, $\tau_{Kr} = -0.2037$, $P = 0.001$ and $K_r = -111$, $\tau_{Kr} = -0.1454$, $P = 0.0257$; Table 3.6). This negative interchange was influenced by rank (Table 3.6), but uninfluenced by proximity (Table 3.7). In mandrills, the interchange of grooming rate received and aggressor-punishment given was near-significant ($K_r = 30$, $\tau_{Kr} = 0.1206$, $P = 0.058$; Table 3.6); although it was influenced by rank and proximity (Tables 3.6 and 3.7). Finally, again in mandrills, grooming rate given was interchanged for victim-punishment received ($K_r = 49$, $\tau_{Kr} = 0.1026$, $P = 0.0498$: Table 3.6). This interchange was neither influenced by rank (Table 3.6) nor proximity, although the latter was the case only at the two closest social distance measures, i.e., C and $P_1$ (Table 3.7).

**Table 3.6** Results of Kr for interchange of aggression, grooming, and punishment*

| **Interchange** | **Species** | **Kr** | **$\tau_{Kr}$** | **P** |
|---|---|---|---|---|
| Aggression x | **G** | 22 | 0.1746 | **0.0873** |
| Grooming (rate) received | **M** | 55 | 0.0885 | **0.0861** |
| *Controlled for Rank* | G | | 0.0323 | 0.4027 |
| | **M** | | 0.0892 | **0.0802** |
| Aggression received x | **G** | 49 | 0.3934 | **0.0005** |
| Grooming (rate) | **M** | 55 | 0.0891 | **0.0727** |
| *Controlled for Rank* | **G** | | 0.1987 | **0.0761** |
| | **M** | | 0.0913 | **0.0707** |
| Aggression x | **G** | 33 | 0.2332 | **0.0299** |
| Grooming (time) received | M | 34 | 0.0388 | 0.2798 |
| *Controlled for Rank* | G | | 0.0000 | 0.4975 |
| Aggression received x | **G** | 51 | 0.3629 | **0.0009** |
| Grooming (time) | M | 31 | 0.0352 | 0.2827 |
| *Controlled for Rank* | G | | 0.1108 | 0.1771 |
| Aggression x | G | 4 | 0.0371 | 0.3962 |
| AG-punishment received | M | -32 | -0.0803 | 0.1238 |
| Aggression received x | **G** | 54 | 0.4820 | **0.0011** |
| AG-Punishment | M | 8 | 0.0205 | 0.3791 |
| *Controlled for Rank* | **G** | | 0.3132 | **0.0723** |
| Aggression x | G | -4 | -0.0360 | 0.4038 |
| VT-punishment received | **M** | -153 | -0.2037 | **0.0010** |
| *Controlled for Rank* | **M** | | -0.1120 | **0.0589** |
| Aggression received x | G | 18 | 0.1597 | 0.1329 |
| VT-Punishment | **M** | -111 | -0.1454 | **0.0257** |
| *Controlled for Rank* | M | | -0.0874 | 0.1349 |
| Grooming (rate) x | G | 3 | 0.0410 | 0.4074 |
| AG-punishment received | **M** | 25 | 0.0987 | **0.0946** |
| *Controlled for Rank* | **M** | | 0.0988 | **0.0959** |
| Grooming (rate) received x | G | 6 | 0.0768 | 0.3222 |
| AG-Punishment | **M** | 30 | 0.1206 | **0.0580** |
| *Controlled* for Rank | **M** | | 0.1223 | **0.0567** |
| Grooming (rate) x | G | 2 | 0.0263 | 0.4539 |
| VT-punishment received | **M** | 49 | 0.1026 | **0.0498** |
| *Controlled for Rank* | **M** | | 0.1053 | **0.0445** |
| Grooming (rate) received x | G | -14 | -0.1781 | 0.1281 |
| VT-Punishment | **M** | 46 | 0.0941 | **0.0912** |
| *Controlled for Rank* | **M** | | 0.0935 | **0.0843** |
| Grooming (time) x | G | 2 | 0.0249 | 0.4446 |
| AG-punishment received | M | 12 | 0.0332 | 0.3151 |
| Grooming (time) received x | G | 8 | 0.0937 | 0.2628 |
| AG-Punishment | **M** | 35 | 0.0998 | **0.0764** |
| *Controlled for Rank* | **M** | | 0.1021 | **0.0695** |
| Grooming (time) x | G | -2 | -0.0239 | 0.4555 |
| VT-punishment received | M | -6 | -0.0088 | 0.4535 |
| Grooming (time) received x | G | -16 | -0.1862 | 0.1296 |
| VT-Punishment | M | -12 | -0.0174 | 0.4076 |

**Kr* and Tau Kr ($\tau_{Kr}$) values give results of tests that examine the relative association between actor matrices and receiver matrices of *different* behaviours, i.e., interchange. Whenever an interchange pattern was found ($P < 0.10$) and any of the behaviour matrices was found to correlate with dominance rank (see Table 3.2), we then ran partial rowwise correlations holding the dominance matrix controlled and give the partial Tau Kr. Geladas (G) = 7; mandrills (M) = 15. P-values < 0.10 are shown in **boldface.**

**Table 3.7** Results of Kr for interchange of aggression, grooming, and punishment*

| Interchange | Species | Kr | $\tau_{Kr}$ | P |
|---|---|---|---|---|
| Aggression x | **G** | 22 | 0.1746 | **0.0873** |
| Grooming (rate) received | **M** | 55 | 0.0885 | **0.0861** |
| *Controlled for C* | G | | -0.1088 | 0.2175 |
| *Controlled for P1* | G | | -0.1277 | 0.1803 |
| *Controlled for P2* | G | | -0.1184 | 0.1972 |
| *Controlled for P3* | G | | -0.1773 | 0.1072 |
| Aggression received x | **G** | 49 | 0.3934 | **0.0005** |
| Grooming (rate) | **M** | 55 | 0.0891 | **0.0727** |
| *Controlled for C* | **G** | | 0.2912 | **0.0184** |
| | **M** | | 0.1111 | **0.0351** |
| *Controlled for P1* | **G** | | 0.2932 | **0.0187** |
| | **M** | | 0.0976 | **0.0603** |
| *Controlled for P2* | **G** | | 0.2777 | **0.0212** |
| | M | | 0.0638 | 0.1551 |
| *Controlled for P3* | **G** | | 0.2726 | **0.0262** |
| | M | | 0.0643 | 0.1470 |
| Aggression x | **G** | 33 | 0.2332 | **0.0299** |
| Grooming (time) received | M | 34 | 0.0388 | 0.2798 |
| *Controlled for C* | G | | -0.1302 | 0.1643 |
| *Controlled for P1* | G | | -0.1211 | 0.1910 |
| *Controlled for P2* | G | | -0.1223 | 0.1873 |
| *Controlled for P3* | G | | -0.1206 | 0.1904 |
| Aggression received x | **G** | 51 | 0.3629 | **0.0009** |
| Grooming (time) | M | 31 | 0.0352 | 0.2827 |
| *Controlled for C* | **G** | | 0.1948 | **0.0456** |
| *Controlled for P1* | **G** | | 0.1836 | **0.0555** |
| *Controlled for P2* | **G** | | 0.1690 | **0.0799** |
| *Controlled for P3* | **G** | | 0.1609 | **0.0842** |
| Aggression x | G | 4 | 0.0371 | 0.3962 |
| AG-punishment received | M | -32 | -0.0803 | 0.1238 |
| Aggression received x | **G** | 54 | 0.4820 | **0.0011** |
| AG-Punishment | M | 8 | 0.0205 | 0.3791 |
| *Controlled for C* | **G** | | 0.4249 | **0.0164** |
| *Controlled for P1* | **G** | | 0.4310 | **0.0148** |
| *Controlled for P2* | **G** | | 0.4234 | **0.0140** |
| *Controlled for P3* | **G** | | 0.4386 | **0.0133** |
| Aggression x | G | -4 | -0.0360 | 0.4038 |
| VT-punishment received | **M** | -153 | -0.2037 | **0.0010** |
| *Controlled for C* | **M** | | -0.2036 | **0.0017** |
| *Controlled for P1* | **M** | | -0.2043 | **0.0012** |
| *Controlled for P2* | **M** | | -0.1992 | **0.0026** |
| *Controlled for P3* | **M** | | -0.1377 | **0.0311** |
| Aggression received x | G | 18 | 0.1597 | 0.1329 |
| VT-Punishment | **M** | -111 | -0.1454 | **0.0257** |
| *Controlled for C* | **M** | | -0.1459 | **0.0212** |
| *Controlled for P1* | **M** | | -0.1459 | **0.0226** |
| *Controlled for P2* | **M** | | -0.1438 | **0.0246** |
| *Controlled for P3* | **M** | | -0.1377 | **0.0340** |

| Interchange | Species | Kr | $\tau_{Kr}$ | P |
|---|---|---|---|---|
| Grooming (rate) x | G | 3 | 0.0410 | 0.4074 |
| AG-punishment received | **M** | 25 | 0.0987 | **0.0946** |
| *Controlled for C* | **M** | | 0.1176 | **0.0321** |
| *Controlled for P1* | **M** | | 0.1147 | **0.0365** |
| *Controlled for P2* | M | | 0.0707 | 0.1223 |
| *Controlled for P3* | **M** | | 0.0899 | **0.0746** |
| Grooming (rate) received x | G | 6 | 0.0768 | 0.3222 |
| AG-Punishment | **M** | 30 | 0.1206 | **0.0580** |
| *Controlled for C* | M | | 0.0579 | 0.2011 |
| *Controlled for P1* | M | | 0.0775 | 0.1454 |
| *Controlled for P2* | M | | 0.0889 | 0.1096 |
| *Controlled for P3* | **M** | | 0.1059 | **0.0753** |
| Grooming (rate) x | G | 2 | 0.0263 | 0.4539 |
| VT-punishment received | **M** | 49 | 0.1026 | **0.0498** |
| *Controlled for C* | **M** | | 0.1176 | **0.0307** |
| *Controlled for P1* | **M** | | 0.1147 | **0.0339** |
| *Controlled for P2* | M | | 0.0707 | 0.1286 |
| *Controlled for P3* | **M** | | 0.0899 | **0.0724** |
| Grooming (rate) received x | G | -14 | -0.1781 | 0.1281 |
| VT-Punishment | **M** | 46 | 0.0941 | **0.0912** |
| *Controlled for C* | **M** | | 0.1113 | **0.0563** |
| *Controlled for P1* | **M** | | 0.1149 | **0.0469** |
| *Controlled for P2* | **M** | | 0.1033 | **0.0633** |
| *Controlled for P3* | **M** | | 0.1044 | **0.0640** |
| Grooming (time) x | G | 2 | 0.0249 | 0.4446 |
| AG-punishment received | M | 12 | 0.0332 | 0.3151 |
| Grooming (time) received x | G | 8 | 0.0937 | 0.2628 |
| AG-Punishment | **M** | 35 | 0.0998 | **0.0764** |
| *Controlled for C* | M | | 0.0285 | 0.3308 |
| *Controlled for P1* | M | | 0.0537 | 0.2091 |
| *Controlled for P2* | M | | 0.0787 | 0.1238 |
| *Controlled for P3* | M | | 0.0829 | 0.1133 |
| Grooming (time) x | G | -2 | -0.0239 | 0.4555 |
| VT-punishment received | M | -6 | -0.0088 | 0.4535 |
| Grooming (time) received x | G | -16 | -0.1862 | 0.1296 |
| VT-Punishment | M | -12 | -0.0174 | 0.4076 |

**Kr* and Tau Kr ($\tau_{Kr}$) values give results of tests that examine the relative association between actor matrices and receiver matrices of *different* behaviours, i.e., interchange. Whenever an interchange pattern was found ($P < 0.10$) and any of the behaviour matrices was found to correlate with each of the four proximity matrices (see Table 3.3), we then ran partial rowwise correlations holding the proximity matrix controlled and give the partial Tau Kr. Geladas (G), N = 7 and mandrills (M), N = 15. P-values < 0.10 are shown in **boldface.**

## Discussion

The groups of geladas and mandrills analysed in the present study differed in four noticeable patterns. Firstly, mandrills performed more dominance and aggressive behaviours than geladas did (Fig. 3.1). Secondly, geladas were more actively engaged in affiliative behaviours, specifically grooming, than mandrills were (Fig. 3.2). Thirdly, when third-parties intervened aggressively in an ongoing agonistic conflict, geladas were more likely than mandrills to support victims (i.e., they targeted or opposed aggressors); that is, compared to mandrills, geladas were more active in punishing aggressors (Fig. 3.3). Finally, although the dominance hierarchy of both species was highly linear, the dominance gradient in the mandrill group was far greater than that of geladas (Fig. 3.4). And this remarkable difference between geladas and mandrills in the steepness of their groups' dominance hierarchy allowed us to test predictions that follow from a biological market trade-model of reciprocity and interchange of aggression, grooming and punishing, which was actually the primary goal of this study.

Even though controversies still remain, the construct dominance, be it assessed at a dyadic level (i.e., dominance relationships within dyads) or at a group level (e.g., steepness and linearity of a group's dominance hierarchy), has proved useful to predict and understand the social behaviour of group-living animals (Bernstein, 1981; de Waal, 1986; Ellis, 1995; Hand, 1986; Majolo, Aureli and Schino, 2012; Majolo *et al.,* 2012; Rowell, 1974; Drews, 1993; van Schaik, 2016; Wade, 1978). In the present study, an individual's standing in the dominance hierarchy was a better predictor of aggression-related behaviours, including dyadic aggression and aggression by third-parties, than affiliation (Tables 3.2 and 3.8). In geladas, an individual's dominance status predicted both the amount of aggression given and received, that is, high-rankers gave more and received less dyadic aggression than lower-ranking group members did, whereas in mandrills it only predicted aggression given. When third-parties intervened aggressively in ongoing dyadic conflicts, dominance rank predicted the rate of punishment given to, and received by, aggressors and victims in mandrills; however, in geladas it only predicted the amount of punishment received by aggressors and victims. In other words, in geladas aggressive interventions on behalf of victims (aggressor punishment) or aggressors (victim punishment) were not as tightly related to the intervener's rank as it was in mandrills. If we interpret aggressive interventions against aggressors, that is, on behalf of victims, as instances of fight-interference or 'policing' (Boehm, 1981, 1994; Kaplan, 1987; Watts, Colmenares and Arnold, 2000; van Rohr *et al.,* 2012), our findings indicate that this behaviour was infrequent indeed in both groups, although it happened more often in the gelada group

(Fig. 3.3), where aggression was less common (Fig. 3.1) and the dominance hierarchy was shallower (Fig. 3.4). On the other hand, affiliative behaviour, which in the present study was assessed through two different measures of grooming, i.e., rate and time, was found to be unrelated to rank in both species; although in geladas, the correlation between rank and the amount of rate and time of grooming given approached statistical significance (Tables 3.2 and 3.8). The finding that grooming was largely unrelated to dominance rank in both groups and unrelated to the group's dominance gradient suggests that grooming was not a 'commodity' that individuals competed for and, as a consequence, its distribution was largely unconstrained by the dominance status of both the groomer and the groomee.

**Table 3.8** Summary of results on correlations between dominance rank and proximity with aggression, grooming and punishment*

| **Behaviour** | **DR** | **C** | **P1** | **P2** | **P3** |
|---|---|---|---|---|---|
| *Aggression given* | **G(+)**<br>**M(+)** | NS<br>NS | NS<br>NS | NS<br>NS | **G(+)**<br>NS |
| *Aggression received* | **G(-)**<br>NS | NS<br>NS | NS<br>NS | NS<br>**M(+)** | NS<br>**M(+)** |
| *Grooming (rate) given* | **G(-)**<br>NS | **G(+)**<br>**M(+)** | **G(+)**<br>**M(+)** | **G(+)**<br>**M(+)** | **G(+)**<br>**M(+)** |
| *Grooming (rate) received* | NS<br>NS | **G(+)**<br>**M(+)** | **G(+)**<br>**M(+)** | **G(+)**<br>**M(+)** | **G(+)**<br>**M(+)** |
| *Grooming (time) given* | **G(-)**<br>NS | **G(+)**<br>**M(+)** | **G(+)**<br>**M(+)** | **G(+)**<br>**M(+)** | **G(+)**<br>**M(+)** |
| *Grooming (time) received* | NS<br>NS | **G(+)**<br>**M(+)** | **G(+)**<br>**M(+)** | **G(+)**<br>**M(+)** | **G(+)**<br>**M(+)** |
| *Aggressor-Punishment given* | NS<br>**M(-)** | NS<br>**M(+)** | NS<br>**M(+)** | NS<br>**M(+)** | NS<br>**M(+)** |
| *Aggressor-Punishment received* | **G(-)**<br>**M(-)** | NS<br>NS | NS<br>NS | NS<br>**M(+)** | NS<br>**M(+)** |
| *Victim-Punishment given* | NS<br>**M(+)** | NS<br>NS | NS<br>NS | NS<br>NS | NS<br>NS |
| *Victim-Punishment received* | **G(-)**<br>**M(-)** | NS<br>NS | NS<br>NS | NS<br>**M(+)** | NS<br>NS |

*DR = dominance rank; C = contact; P1 = <1 arm's reach; P2 = between 1 arm's reach and 2 arms' reach; P3 = between 2 arms' reach and 4 meters. G or M = the correlation was statistically significant ($P < 0.05$) or there was a trend ($0.05 < P < 0.10$). (+) = positive correlation; (-) = negative correlation. NS = non-significant correlation ($P > 0.10$). G = geladas; M = mandrills. See Tables 3.2 and 3.3.

Spending time around some particular others may potentially predict the identity of the members in the group that one is more likely to interact with. For example, one might direct his or her social behaviour preferentially at those who are more often its neighbours. This study shows that this prediction does not necessarily hold. Overall, in both species active affiliation (grooming) was strongly and positively associated with spatial proximity. So, individuals tended to groom and being groomed by those who were their frequent neighbours at any of the social distances analysed (Tables 3.3 and 3.8). Needless to say that grooming involves non-aggressive body contact, so no surprise about this positive relation found between time in association and grooming. However, one might wonder if proximity should also be associated with the likelihood of engaging in aggression. Our findings only rarely supported this association. In geladas, this association was only found between aggression given and the farthest proximity distance ($P_3$), that is, in 1 out of 24 comparisons (Tables 3.3 and 3.8). In mandrills, the pattern observed was rather similar, except in punishing aggressors; here we found that punishers and their aggressor targets tended to be frequent neighbours (in 6 out of 8 comparisons; Tables 3.3 and 3.8).

We tested the assumption that the exchange of aggression should be more strongly unidirectional in the group with a more elevated dominance gradient (Barrett *et al.,* 2002; Henzi *et al.,* 2003). This was confirmed in our study, thus, the steepness of the dominance hierarchy was far greater in the mandrill than the gelada group (Fig. 3.4), and, as predicted, in mandrills, but not in geladas, there was a statistically significant *negative association* between giving and receiving aggression (Tables 3.4 and 3.9). Nonetheless, our analyses revealed that, contrary to expectations (Barrett and Henzi, 2001, 2006), grooming, be it measured as rate or as time, was reciprocal in both groups, independent of dominance rank and proximity, and unrelated to the group's dominance gradient (Tables 3.4, 3.5, 3.9 and 3.10). Reciprocity of grooming is a robust finding documented among females in female bonded groups (see Hemelrijk and Puga-Gonzalez, 2012; Schino and Aureli, 2008a, 2008b for reviews) and among males in male-bonded groups (chimpanzees: Mitani, 2006; Watts, 2002). Schino and Pellegrini (2009) have also reported grooming reciprocity among female mandrills. It is worth noting that the present study found grooming reciprocity in groups containing individuals of both sexes.

**Table 3.9** Summary of results on reciprocity and interchange of aggression, grooming and punishment controlled for dominance rank*

| | **AGR received** | **r-GROO received** | **t-GROO received** | **AG-P received** | **VT-P received** |
|---|---|---|---|---|---|
| AGR given | NS<br>**M(-)** | **G(+)**<br>**M+(+)** | **G(+)**<br>NS | NS<br>NS | NS<br>**M+(-)** |
| r-GROO given | **G+(+)**<br>**M+(+)** | **G+(+)**<br>**M+(+)** | | NS<br>**M+(+)** | NS<br>**M+(+)** |
| t-GROO given | **G(+)**<br>NS | | **G+(+)**<br>**M+(+)** | NS<br>NS | NS<br>NS |
| AG-P given | **G+(+)**<br>NS | NS<br>**M+(+)** | NS<br>**M+(+)** | **G(+)**<br>**M(+)** | |
| VT-P given | NS<br>**M(-)** | NS<br>**M+(+)** | NS<br>NS | | NS<br>**M+(-)** |

*AGR = aggression; r-GROO = rate of grooming; t-GROO = time spent grooming; AG-P = aggressor punishment; VT-P = victim-punishment. G or M = the correlation was statistically significant (P < 0.05) or there was a trend (0.05 < P < 0.10). G+ or M+ = the correlation remained statistically significant (P < 0.05) or there was a trend (0.05 < P < 0.10) after controlling for dominance rank. (+) = positive correlation; (-) = negative correlation. NS = non-significant correlation (P > 0.10). G = geladas, M = mandrills. See Tables 3.4 and 3.6.

**Table 3.10** Summary of results on reciprocity and interchange of aggression, grooming and punishment controlled for proximity

| | **AGR received** | **r-GROO received** | **t-GROO received** | **AG-P received** | **VT-P received** |
|---|---|---|---|---|---|
| AGR given | NS<br>**Mp2p3(-)** | **G(+)**<br>**M(+)** | **G(+)**<br>NS | NS<br>NS | NS<br>**Mcp1p2p3(-)** |
| r-GROO given | **Gcp1p2p3(+)**<br>**Mcp1(+)** | **Gcp1p2p3(+)**<br>**Mcp1p2p3(+)** | | NS<br>**Mcp1p3(+)** | NS<br>**Mcp1p3(+)** |
| t-GROO given | **Gcp1p2p3(+)**<br>NS | | **Gcp1p2p3(+)**<br>**Mcp1p2p3(+)** | NS<br>NS | NS<br>NS |
| AG-P given | **Gcp1p2p3(+)**<br>NS | NS<br>**Mp3(+)** | NS<br>**M(+)** | **Gcp1p2p3(+)**<br>**Mc(+)** | |
| VT-P given | NS<br>**Mcp1p2p3(-)** | NS<br>**Mcp1p2p3(+)** | NS<br>NS | | NS<br>**Mcp1p2p3(-)** |

*AGR = aggression; r-GROO = rate of grooming; t-GROO = time spent grooming; AG-P = aggressor punishment; VT-P = victim-punishment. G or M = the correlation was statistically significant (P < 0.05) or there was a trend (0.05 < P < 0.10). Gcp1p2p3 or Mcp1p2p3 = the correlation remained statistically significant (P < 0.05) or there was a trend (0.05 < P < 0.10) after controlling for the indicated proximity-related measures. C = contact; P1 = <1 arm's reach; P2 = between 1 arm's reach and 2 arms' reach; P3 = between 2 arms' reach and 4 meters. (+) = positive correlation; (-)= negative correlation. NS = non-significant correlation (P > 0.10). G = geladas, M = mandrills. See Tables 3.5 and 3.7.

Most previous tests of the relation between grooming and support (by third-parties) have analysed actor-receiver matrices of *support* given and *support* received. In the present study, however, the actor-receiver matrices consisted of *punishment* given and targeted aggression or *punishment* received (see also de Waal and Luttrell, 1988; Hemelrijk and Ek, 1991; Hemelrijk and Puga-Gonzalez, 2012). That is, they provided information about the *intervener* (supporter) or *punisher* and the *target* (not the supported) individual. Moreover, we made two different punisher-target matrices, one for targets who were aggressors (*aggressor punishment*) and another for targets who were victims (*victim punishment*) in the initial aggressive encounter. Therefore, any third-party aggressive intervention against the aggressor or the victim was actually an instance of victim support or aggressor support, respectively. Unlike the majority of previous studies (see, however, de Waal and Luttrell, 1988; de Waal and Brosnan, 2006; Hemelrijk and Ek, 1991; Hemelrijk and Puga-Gonzalez, 2012; Watts, 1997), this second analysis was thus innovative in two ways. It gave information on the target, not the supported, individual, and it ran separate analyses for patterns of punishment of aggressor *versus* victim targets. We assumed that giving punishment to individuals who are victims in an aggressive interaction and receiving punishment as a victim were likely to exhibit a unidirectional pattern, as interveners were relatively high-rankers and victims were relatively low-ranking individuals (Table 3.2). This was indeed strongly the case, but only in mandrills, as it even held up after controlling for dominance rank and time in proximity (Tables 3.4, 3.5, 3.9 and 3.10). With aggressor punishment, however, it turned out that, in the gelada group, the individuals tended to punish relatively more often those partners from whom they also received more punishment in return. In other words, punishing aggressors and being target of punishment as an aggressor were positively, not negatively, related, although this was independent of proximity, but somewhat influenced by dominance rank (Tables 3.4, 3.5, 3.9 and 3.10). Or, put it another way, in the more egalitarian group of geladas punishment of aggressors was reciprocal as it was likely to elicit counter-punishment from their targets. In mandrills there was also a similar trend, although this was only marginally significant. de Waal and colleagues labelled these counter-aggressive interventions (from targets toward punishers) *contra*-interventions (as opposed to *pro*-interventions on behalf of victims) and *harmful* (as opposed to *beneficial*) interventions (de Waal and Luttrell, 1988; de Waal and Brosnan, 2006; see also Hemelrijk and Ek, 1991; Watts, 1997). They found that contra-interventions (i.e., punishing interveners from whom they have received aggressor punishment in this study) were rather common in chimpanzees, but absent in rhesus and stumptail macaques, and concluded that this could be due to the relatively more egalitarian dominance style of chimpanzees compared to the more despotic of the two macaque species (de Waal and Luttrell, 1988; de Waal and Brosnan, 2006). In this study, aggressive interventions by third-parties were all down the hierarchy (i.e., 'conservative' and 'bridging', Chapais, 1995) in that interveners tended to be the highest-ranking participant in the triad; however, bridging interventions where third-parties supported the victim against the aggressor were more frequent in the group with a lower dominance gradient (gelada group). This could be interpreted to mean that bridging interventions can contribute to smooth power differentials between group members, much as counter-aggression (chapter 4) or aggressive retaliation of third-party punishment can. This idea is supported by a recent study in geladas where aggressive interventions on behalf of victims were found to have a pacifying effect on the levels of agonistic escalation in the group (Pallante, Stanyon, and Palagi, 2016).

In geladas, the *interchange of aggression for grooming* occurred in both directions for grooming time and only in one direction for grooming rate. These patterns were influenced by rank and, in several cases, they were found to be independent of proximity (Tables 3.6, 3.7, 3.9 and 3.10). In the case of mandrills, interchange of aggression for grooming was only marginally significant and only occurred with grooming rate (Tables 3.6, 3.7, 3.9 and 3.10). Similar findings have been reported for Japanese macaques (Schino, Ventura, and Troisi, 2005). These findings indicate that there can be a positive association between these two components of dyadic relationships, although it is unclear what the causal and functional links might be. Indeed, targets of aggression sometimes use grooming as a strategy to lower the probability of renewed attacks from their former aggressors and, eventually, to reconcile with each other after an aggressive confrontation (Arnold *et al.*, 2011; Aureli *et al.,* 2012). However, without an analysis of short-term contingency between aggression and grooming this hypothesized appeasement function cannot be adequately tested (see Cheney and Seyfarth, 2012; Hemelrijk, 1994; Schino *et al.,* 2005; Schino and Aureli, 2009; Schino and Alessandrini, 2015).

In geladas there was *interchange of aggression* received for *punishment* given to aggressors, which did not hold up after controlling for rank. This means that when power differentials are looser, like in punisher-aggressor target dyads of groups with shallow dominance gradients, the two behaviours can be positively associated. Interestingly, this association was independent of proximity (Tables 3.6, 3.7, 3.9 and 3.10). In mandrills there was a *negative* interchange of aggression for punishment of victims in both directions, a pattern which was unrelated to rank or proximity (Tables 3.6, 3.7, 3.9 and 3.10). As predicted, in the group with a steeper dominance hierarchy there was a unidirectional pattern of interchange of aggression and punishment of victims which mirrored the reciprocity of aggression found in this group (see above). That is, individuals punished relatively more often victim targets from whom they received relatively *less* aggression in return (see Hemelrijk and Puga.Gonzalez, 2012). Victims are typically of lower rank than their aggressors and this power differential is even greater with third-party interveners, and in a despotic group like that of mandrills, aggressive retaliation up the hierarchy was rather uncommon (chapter 4).

Our analyses found some support for the hypothesized *negative relation* between *grooming* and *punishment*, a pattern predicted to be more clear-cut when the dominance hierarchy is steeper. Thus, as expected, we did find a negative relation between these two variables, and we did find it only in mandrills, too, but this was only marginally significant (Tables 3.6, 3.7, 3.9 and 3.10). A positive interchange of grooming for support (or other valuable services) has been reported in several species (see Hemelrijk and Puga-Gonzalez, 2012; Schino, 2007; Schino and Aureli, 2008a, 2008b, 2009) and, from the BMT, the prediction has been made that in groups with greater dominance gradient, individuals should be expected to exhibit reduced reciprocity of grooming and increased interchange of grooming for some rank-related service (Barrett and Henzi, 2001, 2006). Tests of this prediction have yielded mixed results and raised questions as to, among others, how to better operationally define a biological market, what time frame is more appropriate to testing its predictions, and how to tackle the issue about its underlying mechanisms (Sánchez-Amaro and Amici, 2015, 2016; Kaburu and Newton-Fisher, 2015, 2016).

Overall, most of the assumptions and predictions we set out to assess and test in the present study (see Introduction) were borne out by the data, however, there were two particularly central predictions that were not supported, although to a different extent. First, we found grooming to be reciprocated in both groups (Tables 3.4-3.5 and 3.9), which means that the dominance gradient did not have the expected effect (prediction *e)*. Second, although our analyses confirmed the predicted negative relation between grooming and punishment in the group with the steeper dominance hierarchy (prediction *k*), however, the correlation was only marginally significant ($0.05 < p < 0.10$). Kaburu and Newton-Fisher (2015) found similar results for male chimpanzees from two communities, that is, grooming was reciprocally exchanged in the two communities, regardless of variation in dominance gradient; and interchange of grooming for agonistic support was observed in the community where the hierarchy was steeper. In a study of reciprocity and interchange among female hamadryas baboons, the authors reported the existence of grooming reciprocity, but no interchange of grooming for any rank-related service, despite the fact that they actively engaged in contest competition for food when this was delivered in a single pile (Leinfelder *et al.*, 2001). However, they did not analyse aggression or agonistic support, and no measure of steepness was worked out; so, more direct comparisons with our study are not possible.

The results obtained in the present study thus add to the existing database of empirical studies on the role of grooming reciprocity and interchange of grooming for agonistic support in the servicing of social bonds and sociality in primates (Cords, 1997; Dunbar, 1984, 1988; Dunbar and Shultz, 2010; Kummer, 1978; Seyfarth and Cheney, 2012; Silk, 2012). It also expands it in that we explored a number of assumptions and predictions that have been less often addressed in other studies of biological markets. Our study was correlational and behavioural scores were collected over a 22 week period. Although this long time frame does not allow to establish contingent relations between aggression, grooming and punishment, both within and across behaviours, recent studies have shown, however, that patterns of grooming reciprocity emerge even when the instances of immediate reciprocity are excluded from analyses (mandrills: Schino and Pellegrini, 2009; capuchins: Schino, Di Giuseppe and Visalberghi, 2009; see also Jaeggi *et al.,* 2013; Schino, Ventura and Troisi, 2003, Schino and Aureli, 2009). The patterns of reciprocity and interchange of aggression, grooming, and punishment reported in this study were assessed at group-level (Hemelrijk, 1990a, 1990b) and over a rather long time frame; the results obtained provide further support for the role of partner choice as central to an understanding of cooperation, bonding and sociality in primates (Campennì and Schino, 2014; Schino and Aureli, 2009, 2016). The biological market framework (Hammerstein and Noë, 2016) can still make important contributions toward uncovering the scaffold mechanisms of bonded sociality (Cheney *et al.,* 2012; de Waal and Suchak, 2010; Hemelrijk and Puga-Gonzalez, 2012; Jaeggi *et al.,* 2013; Schino and Aureli, 2010), even though there are a number of conceptual and methodological issues that need to be more carefully sharpened (Sánchez-Amor and Amici, 2015, 2016).

# CHAPTER 4

# Dominance style and conflict management strategies in geladas *(Theropithecus gelada)* and mandrills *(Mandrillus sphinx)*: A test of the Covariation Hypothesis and the Relational Model

**Abstract.** According to the Covariation Hypothesis many behavioural traits related to a species' dominance style are expected to have undergone correlated evolution. According to the Relational Model, sociality has favoured the evolution of behavioural strategies of conflict management aimed at mitigating the potentially dispersing effects of conflicts of interest that escalate to serious aggression and at restoring the bonds between individuals and the group's cohesion that may have been temporarily disrupted by aggression. This study uses a database of 586 aggressive interactions and 2,931 ensuing social strategies recorded in a group of geladas *(Theropithecus gelada)* and a group of mandrills *(Mandrillus sphinx)* during aggressive conflicts and during post-conflict periods to test predictions that follow from both theoretical frameworks. We found that compared to mandrills, geladas exhibited a more egalitarian dominance style and, as expected, they displayed higher levels of post-conflict affiliation and counter-aggression, and aggressors were as likely as victims to initiate peace-making behaviours. We also found that, as expected, in both species aggressive conflicts were immediately followed by high levels of affiliative interactions between antagonists and by high levels of behavioural indicators of anxiety. Our findings also support the view that aggression and affiliation are group, rather than dyadic, processes so that both antagonist-initiated and third-party initiated interactions need to be taken into account if we are to understand the complexity of group life and the behavioural and cognitive strategies that have evolved to maintain the benefits of sociality in the face of inevitable conflicts of interest between group members.

**Key words**: conflict management strategies, aggression, affiliation, dominance style, covariation hypothesis, relational model, gelada, mandrill.

## Introduction

*Sociality* is known to be an evolved strategy adopted by many animal species to solving more efficiently the problems of survival and reproduction (Alexander, 1974; Wrangham, 1980; van Schaik, 1983, 1989; Dunbar, 1984, 1988; Clutton-Brock, 1989; Lee, 1994; Silk, 2007b, 2012; Majolo, Vizioli and Schino, 2008; Fuentes, 2011; Schülke and Ostner, 2012). However, group-living is not a cost-free solution at all. Rather it brings *social competition* for fitness-enhancing resources into the very social group where individuals interdepend on one another and make, shape, break, and negotiate their partnerships (Dunbar, 1984, 1988; Dunbar and Shultz, 2010; Massen, Sterck, and de Vos, 2010; van Schaik, 1989, 2016). Resources and services of various kinds, including companionship and friendship, skin cleaning, contact comfort, emotional support, sex or protection against social aggression, are limited and have crucial effects on fitness, so group members are expected to engage in a variety of interactions and relationships aimed to successfully and optimally monopolize such resources, inevitably at the expense of pushing other group fellows away from their own optima (Dunbar and Shultz, 2010; Massen *et al.*, 2010; Seyfarth and Cheney, 2012; Silk, 2002; Silk, 2007b, 2012). In essence, then, group life is a scenario where individuals often experience *conflicts of interest* and their behaviour in those contexts should reflect the way they manage their conflicts and balance the costs and benefits of the strategies they play out.

Early studies of conflict resolution focused mainly on the analysis of aggression, as expressed in dyadic interactions, and the assessment of *dominance rank* within dyads, i.e., *dominance relationships*, and within entire groups, i.e., *dominance hierarchies* (Bernstein, 1981; Deag, 1977; Drews, 1993; Richards, 1974; Rowell, 1974; Wade, 1978; see chapter 3). However, researchers soon realized (a) that some aggression can actually have a pacifying function not only among the initial combatants, but also in the group as a whole (Bernstein, 1966, 1976; Bernstein and Sharpe, 1966); (b) that aggression is just one among a wide repertoire of alternative social behaviours that can be deployed during conflicts (de Waal and Roosmalen, 1979, de Waal, 1986; Colmenares and Rivero, 1986); and (c) that many of such aggressive conflicts are rarely dyadic, that is, they tend to involve multiple individuals in a row or simultaneously, each playing different roles (Colmenares and Rivero, 1986). Thus, during aggressive conflicts, initially non-involved third-parties have been reported to aggressively intervene and stop the antagonists' aggressive exchanges (Boehm, 1981, 1994; Colmenares, 1996a; de Waal, 1978a, 1978b; Harcourt and de Waal, 1992; Kaplan, 1977, 1978, 1987; Watts, Colmenares, and Arnold, 2000; van Rohr *et al.*, 2012). During social conflicts and especially very soon after an aggressive interaction has ended former opponents in many social species have also been shown to exhibit an elevated rate of affiliative exchanges with one another (Arnold and Aureli, 2007; Arnold, Fraser and Aureli, 2011; Aureli and de Waal, 2000; Aureli, Cords, and van Schaik, 2002; Aureli *et al.*, 2012; de Waal, 2000a, 2000b; Silk, 2002; van Hooff, 2001). And, finally, it is more frequent than not that during social conflicts the number of participants goes up beyond just two. Thus, initially uninvolved third-parties can be recipients of the former antagonists' aggressive or affiliative behaviours and can intervene on their own initiative directing aggressive or affiliative actions towards the former antagonists or even other third-parties (Aureli *et al.*, 2012; Colmenares, 1996b; Das, 2000; Hinde, 1983; Judge and Mullen, 2005; Petit and Thierry, 1994, 2000; Watts, Colmenares, and Arnold, 2000).

During social conflicts, antagonists and third-parties (bystanders) can display a variety of alternative social strategies to presumably influence conflict outcomes. As already noted, early work on agonistic conflicts was mainly informed by the theoretical construct dominance status. Later work, mainly driven by a more ethologically oriented approach, emphasized the need for a systematic description and classification of the stream of social interactions that actually take place during conflict events. This empirically inductive approach to the study of conflicts was thoroughly developed and successfully applied to the analysis of conflicts in macaques (de Waal, 1976, 1977, 1978a; de Waal *et al.*, 1976) and chimpanzees (de Waal, 1978b; de Waal & van Hooff, 1981; Hemelrijk *et al.*, 1991). Colmenares and Rivero (1986) noted that although many researchers had complained that social relationships could not be properly understood through the isolated analysis of the dyadic components of interactions (Crook, 1970; de Waal *et al.*, 1976; Hinde, 1978; Kummer, 1967, Kummer *et al.*, 1974; Rasmussen, 1981), few had actually taken this key level of analysis, namely, the interactional level, seriously enough. Colmenares and Rivero (1986) also used a similarly inductive approach to describe and classify the social interactions that occur during conflicts in baboons, taken as a case study, and defined several levels of complexity by zooming in and out to/from social interactions (a) the *behavioural actions* (BAs) performed (up to 11 categories of BAs were defined), (b) the *behavioural tactics* (BTs) adopted, defined in terms of the temporal context in which the BAs are deployed (up to 39 BTs were described), (c) the *social strategies* (SSs) used, defined in terms of the direction of the BTs (up to 35 SSs were catalogued), and, finally, (d) the *interaction units* (IUs), that were defined in terms of the complete set of SSs recorded (up to 178 IUs made up the so-called *social ethogram*). The bottom line of the 'what, when, to whom, and type of game' social ethogram proposed by Colmenares and Rivero emphasized the importance of taking into account both the temporal as well as the spatial dimensions of interactions when tackling the study of social relationships and group structure (Colmenares, 1996a, 1996b; Colmenares and Lázaro-Perea, 1994).

However, this inductively oriented approach was short-lived, as it was soon shadowed by later developments in this area of conflict resolution research. de Waal and Roosmalen's (1979) observations of non-violent body contact between former opponents (labelled 'reconciliations') and between antagonists and third-parties (labelled 'consolations') soon after a conflict in a colony of chimpanzees, led de Waal to formulate the reconciliation theory, and much of the work that followed in the next decades was mainly aimed to elaborate this theoretical framework, develop methods of testing its predictions, and conduct observational and experimental studies to test the hypotheses (de Waal, 2000a). In addition to the reconciliation hypothesis proper put forward by de Waal, conflict researchers have articulated several finer-grained models and hypotheses that help to make sense of the occurrence of elevated levels of post-conflict friendly reunions (e.g., the *Relational Model of aggression*, de Waal, 2000a; de Waal and Aureli, 1997), of the reported variation in conciliatory tendency (e.g., the *Valuable Relationship,* Cords and Thurnheer, 1993; Cords and Aureli, 2000), and the functional consequences of reconciling aggressive conflicts in terms of stress-reduction (e.g., the *Uncertainty-Reduction* and the *Integrated* Hypotheses, Aureli, 1997; Aureli, van Schaik, and van Hooff, 1989; Aureli and van Schaik, 1991a), bond-repairing (Cords and Thurnheeler, 1993; Cords and Aureli, 1997; Aureli and Smucny, 1998) or costly signalling of benign intent (Silk, 1997, 1998). Also, following de Waal and Roosmalen (1979) landmark paper, a number of methods were devised to quantitatively assess inter-dyad variation in conciliatory tendency (de Waal and Yoshihara, 1983; Aureli, van Schaik, and van Hooff, 1989; Kappeler and van Schaik, 1992; Colmenares 1996a; Cords, 1993; Veenema, Das, and Aureli, 1994; Butovskaya and Kozintsev, 1999; Logan, Emery, and Clayton, 2013). The field of conflict-resolution research has certainly blossomed over the past few decades, with empirical support for many of its core predictions reported for many species, including nonhuman and human primates (see Aureli and de Waal, 2000; Aureli, Cords, and van Schaik, 2002; Arnold and Aureli, 2007; Arnold, Fraser and Aureli, 2011; Aureli *et al.*, 2012; Colmenares, 1996b, 2006 for reviews), non-primate mammals and birds (see chapter 1: General Introduction).

Some studies of between-species variation in conflict resolution strategies have analysed the influence of socio-ecological and phylogenetic factors (e.g., resource monopolizability, phylogenetic conservatism), as they are claimed to generally shape the characteristics of each species' social system (Clutton-Brock and Janson, 2012; de Waal, 1989; de Waal and Luttrell, 1989; Di Fiore and Rendall, 1994; Dunbar, 1988; Fuentes, 2011; Kamilar and Cooper, 2013; Koenig *et al.*, 2013; Sterck, Watts, and van Schaik, 1997; Schülke and Ostner, 2012; Thierry, 2000, 2004, 2007, 2008, 2013; Thierry *et al.*, 2000, 2008; van Schaik, 1989, 2016). A crucial dimension of a group's social structure is dominance, broadly defined as the ability to monopolize resources in competitive contexts. And groups (and species) can be classified in terms of its predominant so-called *dominance style* (de Waal, 1989a; de Waal and Luttrell, 1989; Flack and de Waal, 2004; Matsumura, 1999), which is typically defined in terms of the frequency, severity and direction of aggressive exchanges, the dominance gradient, the presence of unidirectional and formal status signals of dominance/subordinance, the social tolerance around resources (food, water, partners), and the patterns of conflict resolution (e.g., conciliatory tendency; initiation of conciliatory approaches; types of conciliatory behaviours; presence of consolation and third-party affiliation). Thierry has provided a comprehensive comparative analysis of the *social (dominance) styles* of different species of the genus *Macaca* (Thierry, 2000, 2004, 2007; Berman and Thierry, 2010). To account for the patterns of variation in their *social styles*, Thierry (2000, 2004) formulated the *Covariation Hypothesis* which claims that variation in many behavioural traits is actually correlated and that phylogeny may have a greater impact than ecology (see also Thierry, 2007, 2008, 2013; Thierry *et al.*, 2008; Berman and Thierry, 2010). Thierry has classified *Macaca* species' social styles along a scale of four grades that map onto the phylogenetic tree, from highly *despotic* (contests are typically asymmetric, dominance hierarchy is steep, and interactions are strongly kin-biased) to highly *tolerant* or *egalitarian* (contests are more symmetric, hierarchies are shallower, conciliatory tendencies and social tolerance are higher, and kinship is not that influential).

Most systematic studies of conflict management in primates have been conducted in captive settings, although the few that have been done in the wild have largely confirmed the explanatory principles identified in captive studies (see Aureli, *et al.*, 2002; Aureli *et al.*, 2012; Colmenares, 2006 for reviews). Post-conflict conciliatory behaviours have been documented in geladas by Swedell (1997) and by Leone and Palagi (2010). Leone *et al.* (2010) have described post-conflict 'quadratic affiliation' (Judge and Mullen, 2005) or post-conflict affiliation between third-parties. Pallante, Stanyon, and Palagi (2016) have examined the effect of aggressive interventions and its direction choice on the conflict's outcome. As for mandrills, several researchers have studied mandrill conciliatory behaviour (Otovic *et al.*, 2014; Schino and Marini, 2011), post-conflict affiliation with bystanders (Schino and Marini, 2012), redirected aggression (Schino and Marini, 2014), and post-conflict 'quadratic' both aggression and affiliation between bystanders (Schino and Sciarretta, 2015). Self-scratching as a potential indicator of anxiety or emotional arousal caused by social conflicts has also been analysed in this species by Peignot, Jankowski, and Anderson (2004) and by Schino and Sciarretta (2015).

The goal of the present study is threefold. First, we analysed the patterns of conflict management recorded in two captive groups of cercopithecoid African papionins, the gelada *(Theropithecus gelada)* and the mandrill *(Mandrillus sphinx),* to test predictions from the *Covariation Hypothesis* (Thierry, 2000, 2004; de Waal, 1989a, 1989b). More specifically, we used this comparative database to provide a quantitative assessment of the diversity of social strategies that geladas and mandrills deploy during aggressive conflicts and test the link between a species' dominance or social style and the social strategies the individuals use to manage their aggressive conflicts. Here we mainly focused on (a) the proportion of conflicts that were followed by post-conflict affiliation between former antagonists, (b) which antagonist, i.e., the aggressor or the victim, initiated the post-conflict affiliative behaviour, (c) the proportion of conflicts in which there was counter-aggression, and (d) the proportion of conflicts in which there was re-aggression. Second, we tested the *Relational Model* of conflict resolution (de Waal and Aureli, 1997; de Waal, 2000a, 2000b), according to which soon after a conflict has ended, the levels of affiliation tend to increase as antagonists value their partnership and actively engage in behaviours aimed at repairing the bond temporarily disrupted by the aggressive conflict. Finally, we assessed the importance of third-parties by analysing their role as recipients of the former antagonists' behaviour or as active interveners in the latter's ongoing aggressive exchanges (Aureli *et al.*, 2012; Das, 2000; Watts *et al.*, 2000). Here we analysed the nature of the behaviours involved, namely, aggression and affiliation, and the identity of actors and recipients (i.e., aggressors, victims or third-parties).

## Material and Methods

### *Study groups and housing*

The present study was conducted from October 2010 until April 2011 at La Vallée des Singes, a large monkey and ape park located in Romagne (France). Subjects were the members of two groups of cercopithecoid African papionins, *Theropithecus gelada* and *Mandrillus sphinx*, housed in roughly similar naturalistic settings in captivity. The group of geladas was made up of 9 individuals: one adult male, two adult females, two subadult males, one juvenile male, one juvenile female, one yearling female and one infant male (Table 4.1). The group of mandrills comprised 17 individuals: two adult males, eight adult females, three subadult males, two subadult females, and two infant females (Table 4.1). The two groups' enclosures consisted of an indoor facility, not visible to visitors, and an outdoor compound equipped with everything necessary to allow individuals to move freely along all three dimensions (see Figure 2.1 in chapter 2). They included live and dead trees, big rocks, dens, wooden structures built with trunks placed in different positions and interconnected at different levels. The geladas' indoor area was divided into five interconnected rooms 5.30m x 5.80m. It was connected through a hatch system, which was always opened during the periods of data collection to a 2,800m$^2$ outdoor exhibit surrounded by water moat and visible to visitors. This open-air outdoor compound, which circled the indoor zone, had predominantly herbaceous vegetation with several trees and a wooden structure 4 meters high and 15 meters long. The mandrills' indoor area was also divided into five inter-connected rooms 16.80m x 12.10m with several wooden structures. It was connected through a hatch system, also opened during the sessions of data collection, to a 3,500m$^2$ outdoor exhibit, visible to visitors and surrounded by a water moat and the indoor area. This open-air outdoor area was densely vegetated (shrubs and trees) and included wooden structures and platforms above the ground.

**Table 4.1** Subjects of Study*

| **Individual**[1] | **Species** | **Sex** | **Age Class**[2] | **Observations** |
|---|---|---|---|---|
| Bongo (B) | Gelada | M | Adult (7) | Alpha male. Father of Saala, Dashan, Lengay and Haile |
| Lena (L) | Gelada | F | Adult (12) | Alpha female. Mother of Axoun, Saala and Lengay |
| Axoun (AX) | Gelada | M | Subadult (5) | |
| Saala (S) | Gelada | F | Juvenile (3) | |
| Ute (U) | Gelada | F | Adult (11) | Mother of Okoume, Dashan and Haile |
| Okoume (OK) | Gelada | M | Subadult (5) | |
| Dashan (D) | Gelada | M | Juvenile (3) | |
| Haile (H) | Gelada | F | Yearling (1) | |
| Lengay (LG) | Gelada | M | Infant (0.4) | |
| Zoulou (Z) | Mandrill | M | Adult (17) | Alpha male. Father of Amala, Mpassa, Mambassa, Okandja, Nouanda, Nyombé, Lekedi, Mboko, Ebaka, Leny, Natiwe and Mkoa |
| Nina (N) | Mandrill | F | Adult (16) | Alpha female. Mother of Amala, Mpassa, Mambassa, Okandja and Nouanda |
| Nouanda (NO) | Mandrill | F | Adult (9) | |
| Mambassa (MA) | Mandrill | F | Adult (7) | |
| Okandja (OK) | Mandrill | M | Subadult (6) | |
| Mpassa (MP) | Mandrill | F | Adult (5) | |
| Amala (AM) | Mandrill | F | Subadult (4) | |
| Nicky (NI) | Mandrill | F | Adult (14) | Mother of Nyombe, Lekedi and Natiwe |
| Nyombe (NY) | Mandrill | F | Adult (9) | |
| Lekedi (LK) | Mandrill | M | Subadult (6) | |
| Csilla (CS) | Mandrill | F | Adult (14) | Mother of Mboko, Ebaka, Leny and Mkoa |
| Ebaka (EB) | Mandrill | F | Adult (9) | |
| Mboko (MB) | Mandrill | M | Subadult (8) | |
| Leny (LE) | Mandrill | F | Subadult (4) | |
| Nico (NC) | Mandrill | M | Adult (12) | |
| Natiwe (NAT) | Mandrill | F | Infant (1) | |
| Mkoa (MK) | Mandrill | F | Infant (1) | |

*Sources: Charpentier *et al.* (2004); Dunbar (1980); Dunbar & Dunbar (1975); Kawai *et al.* (1983); Laidre & Yorzinski (2005); Leone & Palagi (2010).

[1] Code name in parentheses

[2] Years of age in parentheses

In addition to the vegetation available in the enclosures that individuals of both groups could consume *ad libitum*, geladas were fed four times per day (8.45 a.m., 11.45 a.m., 2.30 p.m. and 4 p.m.), and their diet included grass, vegetables, grains and pellets. Mandrills were fed six times per day (8.30 a.m., 12 a.m., 2.30 p.m., 3.30 p.m., 4.30 p.m. and 5.30p.m.); their diet included fruits, nuts, vegetables, grains and pellets. For both species water was always available *ad libitum*.

### *Data collection: behavioural catalogue, and sampling and recording methods*

The ethograms used in this study were based on those used in previous studies of geladas (Bernstein, 1975; Dunbar and Dunbar, 1975; Mancini and Palagi, 2009) and mandrills (Brockmeyer *et al.*, 2015; Chang *et al.*, 1999; Feistner, 1989; Mellen, Litlewood, Barrow, and Stevens, 1981; Peignot, Jankowski, and Anderson, 2004; Pansini, 2006), and included three *behavioural categories*: aggression (for example, threatening gestures, lunge, chase, slap, push, bite), affiliation (for example, affinitive gestures, embrace, touch, groom), and self-directed behaviour (self-scratch, self-groom, body-shake). The behavioural data analysed in this chapter were collected via focal-animal and focal-group sampling (Altmann, 1974; Dunbar, 1976; Hinde, 1973; Lehner, 1996; Martin and Bateson, 2007). Focal-animal and focal-group follows were 10 min long. The behavioural observations were directly recorded on previously designed check sheets that contained 40 rows, each representing 15s time intervals, and 2 columns to write down focal-animal *versus* focal-group observations side by side, and the recording method was the continuous one (Altmann, 1974; Dunbar, 1976; Lehner, 1996; Martin and Bateson, 2007). All the records included information about the identity of the interacting individuals and their role (initiator, receiver, and third-party) in the interaction. In aggressive interactions, the initiator was labelled as aggressor (AG) and the target of the aggressor's behaviour as the victim (VT). An aggressive intervention was recorded when an initially uninvolved bystander or third-party directed aggressive behaviours towards the aggressor or the victim in an ongoing aggressive interaction.

The behavioural records were collected in two different contexts, during conflicts (Cs) and during post-conflicts (PCs). They were all collected outside feeding situations. A conflict was considered to begin when one individual (dubbed the aggressor) directed an aggressive behaviour at another (dubbed the victim). Conflict duration was variable and was considered to have ended when the aggressor and the victim of the initial conflict stopped being involved in any further agonistic (aggressive or submissive) interaction with each other or with third-parties for at least two minutes. The period after a conflict (i.e., the PC-period), however, was limited to a maximum of 5 minutes. In both contexts the behaviour of the original antagonists (A and B), and of any involved third-party (C) was monitored and recorded as already indicated. If a new conflict (involving individuals other than the original antagonists) erupted during a post-conflict period, efforts were made to carry on the recording of the PC interactions and, at the same time, to collect the interactions between the antagonists involved in the new conflict. If this was not possible, collecting post-conflict data was given priority. The period of data collection went on over 22 weeks, altogether, totalling 241 hours (geladas: 115

hours; mandrills: 126 hours). In each group, individuals younger than 1.5 years of age were never sampled. Also, in the mandrill group there was one individual who never initiated an aggressive interaction, so in the analyses sample sizes were 7 for geladas and 14 for mandrills.

### *Behavioural measures and data analyses*

The behavioural interactions thus collected were classified in terms of two major parameters (Colmenares and Rivero, 1986; Colmenares, 1996a). First, the *role* fulfilled by each participant in the interaction. In dyadic interactions, the roles were the *aggressor* (or A) and the *victim* (or B), that is the target of the aggressor' behaviour. In triadic (or polyadic) interactions, in addition to the two aforementioned roles there was another key role, namely the *third-party* (or C). This was fulfilled by individuals who, although initially non-involved, as the conflict progressed, ended up as conflict participants. This later involvement could take two different forms. Third-parties could actively intervene by directing behaviours at the initial aggressor, at the victim, or at both antagonists; or they could become themselves targets of behaviours initiated by the aggressor or the victim. Second, the type and the direction of the behaviours deployed by the antagonists or by the third-parties. Table 4.2 lists the various social strategies that were coded and analysed in the present study. The category self-directed behaviour analysed in this paper consisted of three different elements: self-groom, self-scratch, and body-shake. The two latter elements were combined into a single category in the analyses (SR-SHB).

**Table 4.2** Catalogue of social strategies *

| **Social strategy** | **Notation** | **Definition** |
|---|---|---|
| Aggression (AG) | A→B | A directs aggressive behaviour at B |
| Counter-aggression (CAG) | B →A | B responds by directing aggressive behaviour at A |
| Re-aggression (RAG) | A →B | A renews his/her aggressive behaviour towards B |
| Side-directed aggression (SDAG) | A →C | A directs aggressive behaviour at C |
| Redirected aggression (RDAG) | B→C | B directs aggressive behaviour at C |
| Aggressive intervention ($AGI_A$) | C→A | C directs aggressive behaviour at A |
| Aggressive intervention ($AGI_B$) | C→B | C directs aggressive behaviour at B |
| Affiliation unidirectional ($AFU_A$) | A→B | A directs affiliative behaviour at B |
| Affiliation unidirectional ($AFU_B$) | B→A | B directs affiliative behaviour at A |
| Side-directed affiliation (SDAF) | A→C | A directs affiliative behaviour at C |
| Redirected affiliation (RDAF) | B→C | B directs affiliative behaviour at C |
| Affiliative intervention ($AFI_A$) | C→A | C directs affiliative behaviour at A |
| Affiliative intervention ($AFI_B$) | C→B | C directs affiliative behaviour at B |

* A and B are the initial antagonists. A is the "aggressor" and B is the "victim". C is the third-party (see text for details).

The database of aggressive interactions that initiated an agonistic conflict and, therefore, marked the beginning of the recording of conflict and post-conflict interactions was 195 for geladas (N = 7 individuals) and 391 for mandrills (N = 14 individuals). Table 4.3 provides the actual number of instances of each of the social strategies that were collected during conflicts and during post-conflicts in geladas and mandrills.

**Table 4.3** Instances recorded of each social strategy in geladas and mandrills

| Social Strategy * | Geladas Conflict | Geladas Post-Conflict | Mandrills Conflict | Mandrills Post-Conflict |
|---|---|---|---|---|
| CAG | 69 | 4 | 33 | 0 |
| RAG | 78 | 2 | 234 | 7 |
| SDAG | 56 | 16 | 64 | 20 |
| RDAG | 45 | 8 | 46 | 13 |
| AGI | 137 | 5 | 241 | 18 |
| AGI$_A$ | 66 | 4 | 21 | 6 |
| AGI$_B$ | 71 | 1 | 220 | 12 |
| AFU | 9 | 100 | 28 | 58 |
| AFU$_A$ | 5 | 59 | 21 | 29 |
| AFU$_B$ | 4 | 41 | 7 | 29 |
| SDAF | 7 | 133 | 109 | 386 |
| RDAF | 11 | 108 | 35 | 179 |
| AFI | 15 | 180 | 115 | 362 |
| AFI$_A$ | 12 | 96 | 64 | 208 |
| AFI$_B$ | 3 | 84 | 51 | 154 |
| SGR | 4 | 52 | 20 | 191 |
| SR/SHB | 9 | 181 | 24 | 238 |

* See Table 4.2 for codes of social strategies.

The scores analysed in this paper were proportions or percentages of occurrence of the various social strategies per conflict initiated. More specifically, for each individual we worked out how many times she or he performed any of the aggressive or affiliative behaviours in relation to the total number of conflicts in which he or she was a participant. We ran separate, within-species analyses to assess the proportion of each social strategy during conflicts *versus* post-conflicts (i.e., C *vs* PC) in geladas and mandrills. We also compared the proportion of aggressive *versus* affiliative strategies during conflicts, on the one hand, and during post-conflicts, on the other. In these analyses we used the Friedman's non-parametric test ($\chi_r^2$) as there were more than 2 aggressive and affiliative strategies within each context, and the Wilcoxon paired-sample test (T) when the aggressive and affiliative strategies were compared within each context (Hawkins, 2005; Neave and Worthington, 1988; Siegel and Castellan, 1988; Zar, 1999). In the comparative analyses between species, we used the Mann-Whitney two-independent samples test (U) (Neave and Worthington, 1988; Siegel and Castellan, 1988; Zar, 1999). These analyses were also run on the scores of the two self-directed behaviours studied. In all the analyses the critical level of significance ($\alpha$) was set at $p < 0.05$. When post-hoc multiple comparisons were made, we adjusted the level of significance using Bonferroni correction. Although some authors have recommended the overall $\alpha$-level of significance be raised in this context (Neave and Worthington, 1988), we decided to keep it at 5%. This means that our analyses were highly conservative with regards to the probability of rejecting the null hypothesis. Thus, although we will report as statistical significant differences only those statistical results that fulfilled the criterion of reaching a p-value $< 0.05$, on occasions we will also report results that reached a p-value $\leq 0.10$ as marginally significant. We run all the analyses on SPSS version 20.

# Results

## *Geladas*

During agonistic conflicts, geladas did not use the five aggressive strategies analysed equally often (Friedman's test, $\varkappa_r^2 = 11.65$, df= 4; n= 7: $p = 0.02$; Fig. 4.1a). *Aggressive intervention* (AGI) was the most frequent strategy, as it occurred in 75% of conflicts. At the other extreme, occurring just in 24% and 27% of conflicts, there were *side-directed aggression* (SDAG) and *redirected aggression* (RDAG), respectively. In the post-hoc pairwise comparisons (Wilcoxon's test), AGI was found to be statistically significantly more frequent than RDAG ($z = -2.57$, $p = 0.02$) and SDAG ($z = -2.29$, $p = 0.07$, NS). Aggressive interveners were found to be as likely to target aggressors as victims ($AGI_A$ vs $AGI_B$, 42.61% vs 32.79%, $p > 0.05$, NS; Fig. 4.2a). In contrast, during post-conflict observations, neither the proportion of the different aggressive strategies, nor the direction of third-parties' aggressive interventions were found to differ from a random distribution, even though the differences approached statistical significance in both cases ($\varkappa_r^2 = 7.6$, df= 4; n= 7: $p = 0.10$, NS; Fig. 4.1b; $z = -1.60$, $p = 0.11$, NS; Fig. 4.2b).

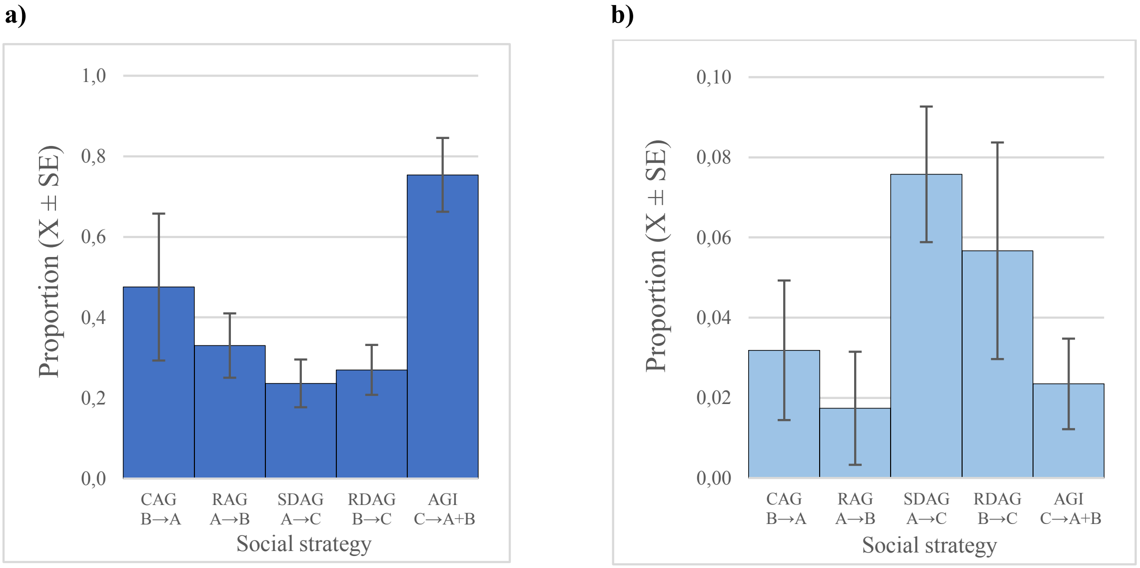


**Figure 4.1** Aggressive strategies used by geladas (a) during conflicts, and (b) post-conflicts.

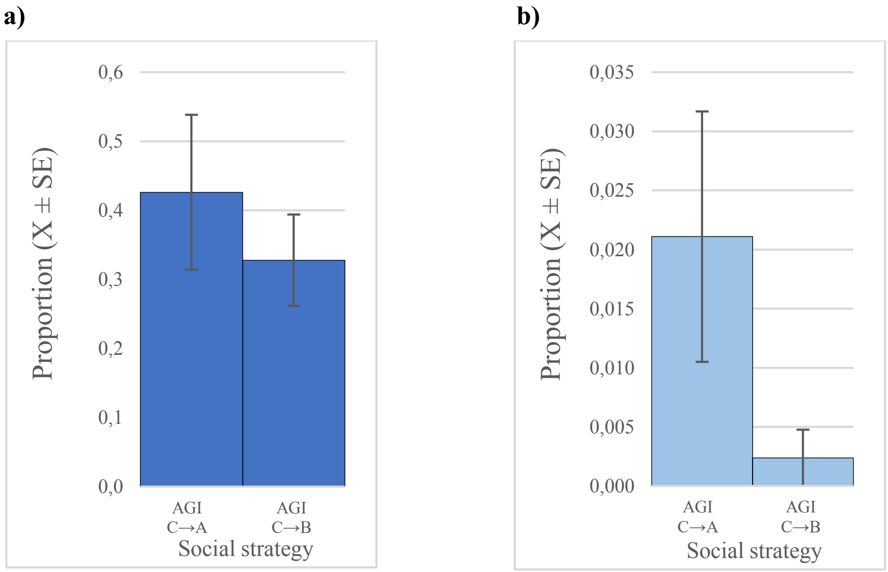


**Figure 4.2** Strategies of aggressive intervention against aggressors and against victims used by geladas (a) during conflicts and (b) post-conflicts.

All the aggressive strategies were more frequent during conflicts than post-conflicts (i.e., conflict/post-conflict ratios were > 1; Table 4.4) and this difference was statistically significant: CAG*c* > CAG*pc* (47.5% vs 3.2%; p = 0.008), RAG*c* > RAG*pc* (33% vs 1.7%; p = 0.02), SDAG*c* > SDAG*pc* (23.6% vs 7.6%; p = 0.03), RDAG*c* > RDAG*pc* (27% vs 5.7%; p = 0.008), AGI*c* > AGI*pc* (75.4% vs 2.3%; p = 0.008), AGI$_A$*c* > AGI$_A$*pc* (42.6% vs 2.1%; p= 0.008), and AGI$_B$*c* > AGI$_B$*pc* (32.8% 0.2%; p= 0.008).

**Table 4.4** Ratios of social (aggressive and affiliative) strategies exhibited during conflicts and post-conflicts, in geladas and mandrills *

| | **Geladas** | | **Mandrills** | |
|---|---|---|---|---|
| **Strategy** | **Conflict** | **Post-conflict** | **Conflict** | **Post-conflict** |
| CAG | **14.89** | | **in C only** | |
| RAG | **18.97** | | **38.43** | |
| SDAG | **3.12** | | **3.03** | |
| RDAG | **4.75** | | **1.77** | |
| AGI$_{A+B}$ | **32.08** | | **11.23** | |
| AGI$_{A}$ | **20.19** | | **3.23** | |
| AGI$_{B}$ | **136.58** | | **15.71** | |
| AFU$_{A+B}$ | 0.08 | | 0.30 | |
| AFU$_{A}$ | 0.03 | | **1.10** | |
| AFU$_{B}$ | 0.15 | | 0.12 | |
| SDAF | 0.04 | | 0.25 | |
| RDAF | 0.09 | | 0.06 | |
| AFI$_{A+B}$ | 0.08 | | 0.29 | |
| AFI$_{A}$ | 0.17 | | 0.34 | |
| AFI$_{B}$ | 0.02 | | 0.27 | |

* AG: aggressive strategies; AF: affiliative strategies. Scores over 1 mean that they were more frequent during conflicts than post-conflicts (i.e., C > PC, in boldface), under 1 that they were more frequent during post-conflicts than conflicts (PC > C).

The variation in the proportions of the four affiliative strategies used by geladas was not statistically significant, neither during conflicts ($\varkappa_r^2 = 4.57$, df= 4; n= 7: $p > 0.05$, NS; Fig. 4.3a), nor during post-conflicts ($\varkappa_r^2 = 1.21$, df= 4; n= 7: $p > 0.05$, NS; Fig. 4.3b). The four affiliative strategies exhibited a similar pattern in both contexts, with *affiliative intervention* (AFI) being the most frequent in both cases, and *side-directed affiliation* (SDAF) the least common. Although there was no statistically significant trend, either, in both contexts aggressors were as likely as victims to *initiate affiliation* ($AFU_A$ and $AFU_B$), although this bias was slightly stronger and reversed during post-conflicts than conflicts (conflicts: $AFU_B > AFU_A$, Fig. 4.4a; post-conflicts: $AFU_A > AFU_B$, 4.4b). The direction of affiliative interventions was also different in each context, but only approached statistical significance during conflicts ($p = 0.14$, NS), in which third-parties tended to target aggressors over victims ($AFI_A > AFI_B$, Fig. 4.4a).

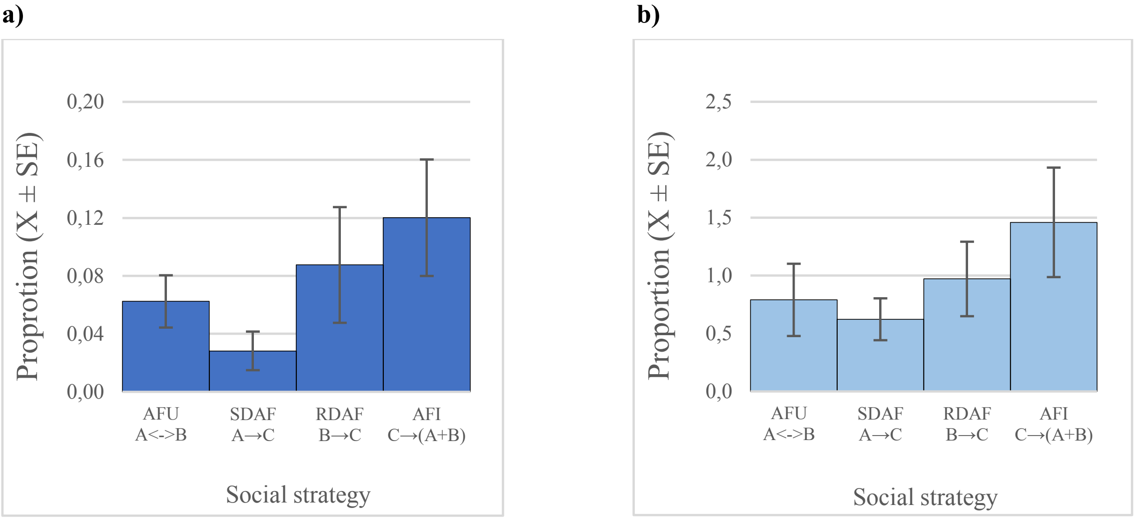


**Figure 4.3** Affiliative strategies used by geladas (a) during conflicts and (b) post-conflicts.

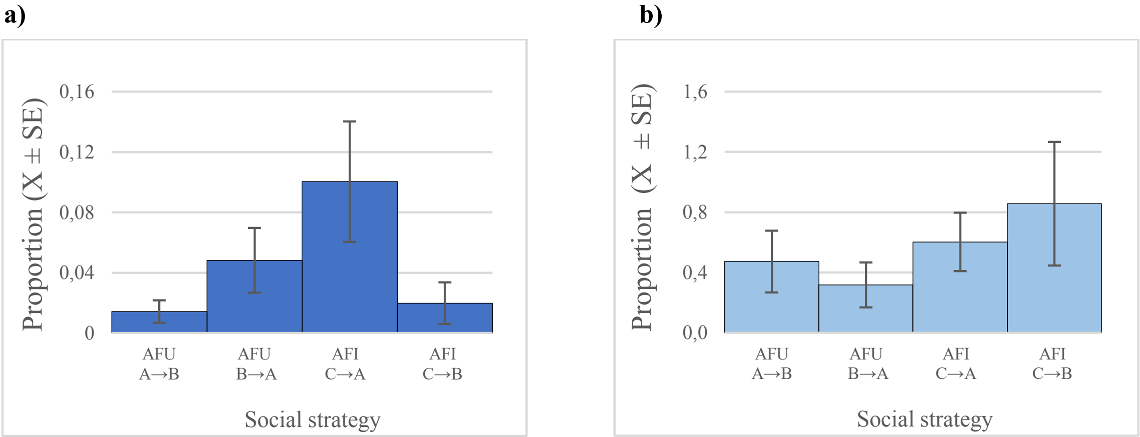


**Figure 4.4** Directionality of affiliation and strategies of affiliative intervention towards aggressors and towards victims used by geladas (a) during conflicts, and (b) post-conflicts.

All the affiliative strategies were more frequent during post-conflict observations than during conflicts (i.e., conflict/post-conflict ratios < 1; Table 4.4) and except one that was only marginally statistically significant, the rest of the differences were highly statistically significant: AFU*c* < AFU*pc* (6.24% vs 79%, p = 0.02); $\mathrm{AFU}_{\mathrm{A}}c < \mathrm{AFU}_{\mathrm{A}}pc$ (1.42% vs 47%, p = 0.05); $\mathrm{AFU}_{\mathrm{B}}c < \mathrm{AFU}_{\mathrm{B}}pc$ (4.8% vs 31.7%, p = 0.08, NS); SDAF*c* < SDAF*pc* (2.8% vs 62%, p = 0.008); RDAF*c* < RDAF*pc* (8.7% vs 97%, p = 0.008), AFI*c* < AFI*pc* (12% vs 145%, p = 0.008); $\mathrm{AFI}_{\mathrm{A}}c < \mathrm{AFI}_{\mathrm{A}}pc$ (10% vs 60%, p = 0.02), and $\mathrm{AFI}_{\mathrm{B}}c < \mathrm{AFI}_{\mathrm{B}}pc$ (2% vs 85.6%; p = 0.008).

The two categories of self-directed behaviour analysed were found to be more frequent during post-conflict than conflict periods (SGR*pc* > SGR*c*, 56% vs 6.43 %, p = 0.02; SR-SHB*pc* > SR-SHB*c*, 30% vs 5%, p = 0.008; Fig. 4.11).

*Mandrills*

The proportions of the five aggressive strategies used by mandrills when they were engaged in an agonistic conflict were markedly different (Friedman's test, $\varkappa_{\mathrm{r}}^{2}$ = 25.42, df= 4; n= 14: p < 0.001; Fig. 4.5a). *Redirected aggression* (RAG) and *aggressive intervention* (AGI) were the two strategies most frequently observed (60% and 48%, respectively), and *side-directed aggression* (SDAG) was the rarest strategy (7.8%). The post-hoc comparisons yielded many statistically significant differences: RAG > SDAG (z= 1.93, p = 0.013); RAG > CAG (z= -1.89, p = 0.015); RAG > RDAG (z= 1.60, p = 0.072); AGI > SDAG (z= -2.0, p = 0.008); AGI > CAG (z= -1.94, p = 0.010); and AGI > RDAG (z= -1.68, p = 0.05). Aggressive interveners targeted victims far more than they did aggressors ($\mathrm{AGI}_{\mathrm{B}} > \mathrm{AGI}_{\mathrm{A}}$, 43.2% vs 5%, z= 3.06, p = 0.002; Fig. 4.6a). During post-conflict observations, the proportions of the different aggressive strategies also differed from chance ($\varkappa_{\mathrm{r}}^{2}$ = 10.85, df= 4; n= 15: p = 0.028; Fig. 4.5b). Nevertheless, no pairwise comparisons reached statistical significance. The most frequent strategy was *redirected aggression* (RDAG, 9.5%), and no single instance of *counter-aggression* (CAG) was ever observed. On the other hand, aggressive interveners were also observed to target more often victims than aggressors ($\mathrm{AGI}_{\mathrm{B}} > \mathrm{AGI}_{\mathrm{A};}$ Fig. 4.6b), however, in this context the difference was not statistically significant (p = 0.33, NS).

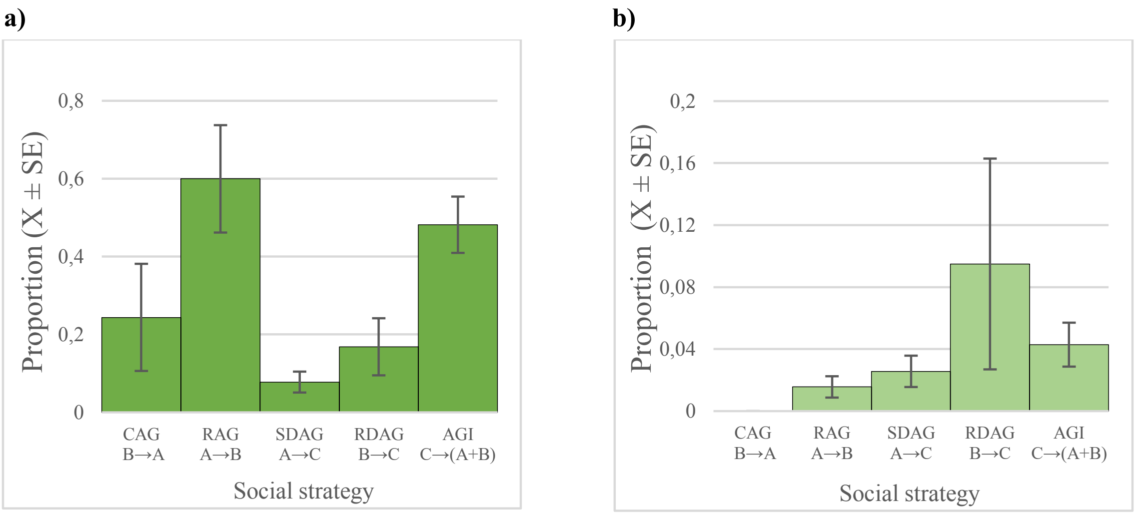


**Figure 4.5** Aggressive strategies used by mandrills (a) during conflicts, and (b) post-conflicts.

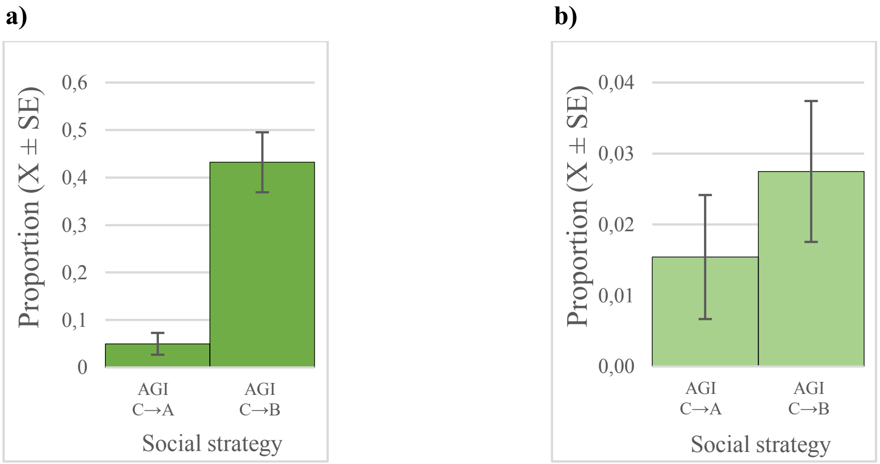


**Figure 4.6** Strategies of aggressive intervention against aggressors and against victims used by mandrills (a) during conflicts and (b) post-conflicts.

All the aggressive strategies were more frequent during conflicts than post-conflicts (i.e., conflict/post-conflict ratios were > 1; Table 4.4), although some of the differences did not reach statistical significance: CAG*c* > CAG*pc* (24.4% vs 0%; $p = 0.002$), RAG*c* > RAG*pc* (60% vs 1.6%; $p < 0.001$), SDAG*c* > SDAG*pc* (7.8% vs 2.6%; $p = 0.02$), RDAG*c* > RDAG*pc* (16.8% vs 9.5%; $p = 0.07$, NS), AGI*c* > AGI*pc* (48.2% vs 4.3%; $p < 0.001$), $\mathrm{AGI}_{A}c > \mathrm{AGI}_{A}pc$ (5% vs 1.5%; $p = 0.12$, NS), and $\mathrm{AGI}_{B}c > \mathrm{AGI}_{B}pc$ (43.2% vs 2.7%; $p < 0.001$).

The four affiliative strategies used during conflicts were performed at different rates, but these differences did not reach statistical significance ($\chi_r^2 = 4.54$, df= 4; n= 15: $p > 0.05$, NS; Fig. 4.7a). The most frequent strategy observed was *affiliative intervention* (AFI, 23.3%) and the one that was least recorded was *affiliation between opponents* (AFU, 7.2%), which was initiated by aggressors more than victims (AFU$_A$ > AFU$_B$, NS; Fig. 4.8a). In contrast, during post-conflicts the individuals used the affiliative strategies at different rates ($\varkappa_r^2$ = 14.2, df= 4; n= 14: p = 0.003; Fig. 4.7b). The only post-hoc comparison that reached statistical significance was *affiliative intervention* versus *affiliation between opponents* (AFI > AFU, 23.3% vs 4.7%, z= -1.75, p = 0.002). Although the victims tended to initiate affiliation with aggressors more often than the other way around (AFU$_B$ > AFU$_A$) and affiliative interveners aimed at victims more than aggressors (AFI$_B$ > AFI$_A$), in neither case were the differences statistically significant (19.7% vs 4.3% and 45% vs 33%; NS).

All of the affiliative strategies but one, *initiation of affiliation by the aggressor* (AFU$_A$), were more frequent during post-conflict observations than during conflicts (i.e., conflict/post-conflict ratios < 1; Table 4.4). Nevertheless, not all them were statistically significant: AFU*c* < AFU*pc* (7.2% vs 24%, p= 0.10, NS); AFU$_A$*c* < AFU$_A$*pc* (4.7% vs 4.3%, NS); AFU$_B$*c* < AFU$_B$*pc* (2.5% vs 19.8%, NS); SDAF*c* < SDAF*pc* (13.2% vs 52%, p = 0.001); RDAF*c* < RDAF*pc* (12% vs 1.79%, p = 0.005), AFI*c* < AFI*pc* (23.3% vs 78%, p = 0.001); AFI$_A$*c* < AFI$_A$*pc* (11.3% vs 33%, p = 0.005), and AFI$_B$*c* < AFI$_B$*pc* (12% vs 45%; p= 0.009).

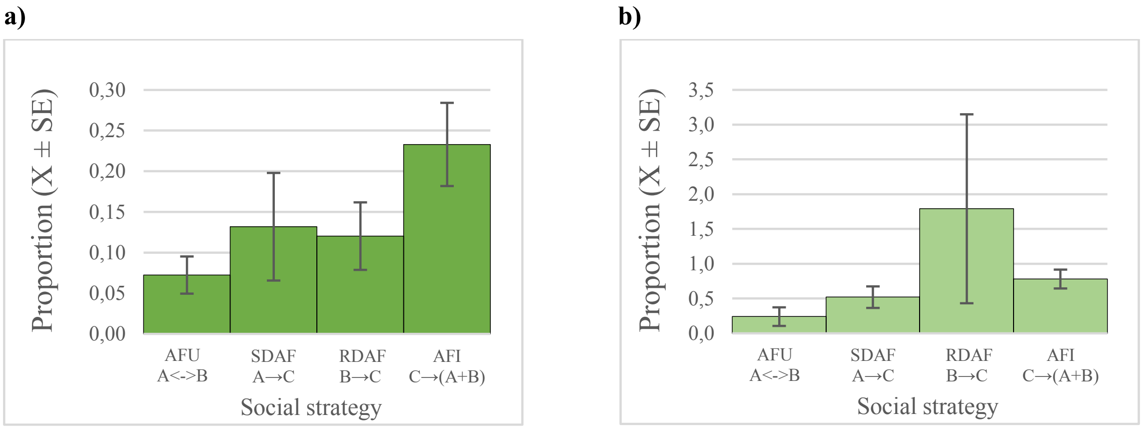

**a)**
**b)**

**Figure 4.7** Affiliative strategies used by mandrills (a) during conflicts and (b) post-conflicts.

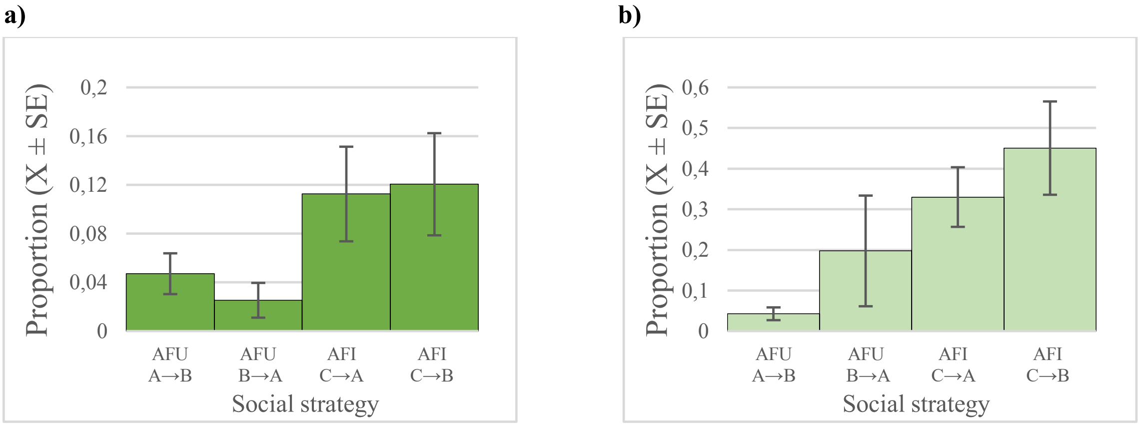

**a)**
**b)**

**Figure 4.8** Directionality of affiliation and strategies of affiliative intervention towards aggressors and towards victims used by mandrills (a) during conflicts, and (b) post-conflicts.

Like in geladas, the two categories of self-directed behaviour analysed were found to be more frequent during post-conflict than conflict periods (SGR*pc* > SGR*c*, 72.3% vs 7.8%, p = 0.001; SR-SHB*pc* > SR-SHB*c*; 102% vs 7.14%, p < 0.001; Fig. 4.11).

### *Geladas* versus *Mandrills*

During conflicts, geladas differed from mandrills in their rates of five (out of 7) aggressive strategies (Fig. 4.9): CAG (geladas > mandrills, z= -2.2, p = 0.02); SDAG (geladas > mandrills, z= -2.28, p = 0.02); RDAG (geladas > mandrills, z= -1.8, p = 0.07, NS); AGI (geladas > mandrills, z= -1.94, p = 0.05); AGI$_A$ (geladas > mandrills, z= -3.37, p < 0.001). During post-conflicts, these differences were only observed in three aggressive strategies (Fig. 4.9b): CAG (geladas > mandrills, z= -2.57, p = 0.02); SDAG (geladas > mandrills, z= -2.0, p = 0.04), and AGI$_B$ (mandrills > geladas, z= -1.7, p = 0.09, NS). Overall, geladas used more aggressive strategies at greater rates than mandrills (5/7 during conflicts and 4/7 during post-conflicts, see Table 4.5).

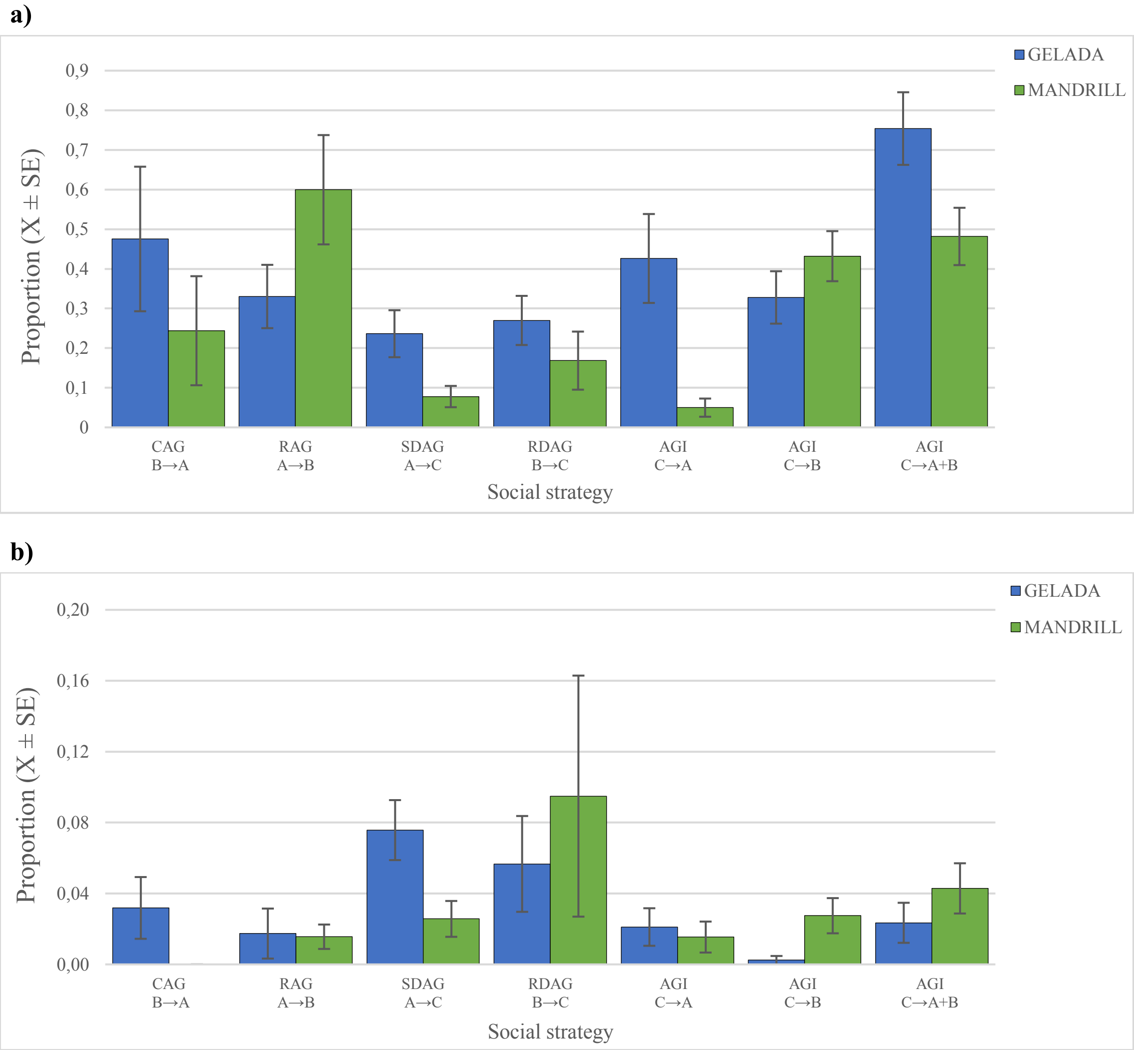


**Figure 4.9** Comparison of aggressive strategies used by geladas and mandrills (a) during conflicts, and (b) post-conflicts.

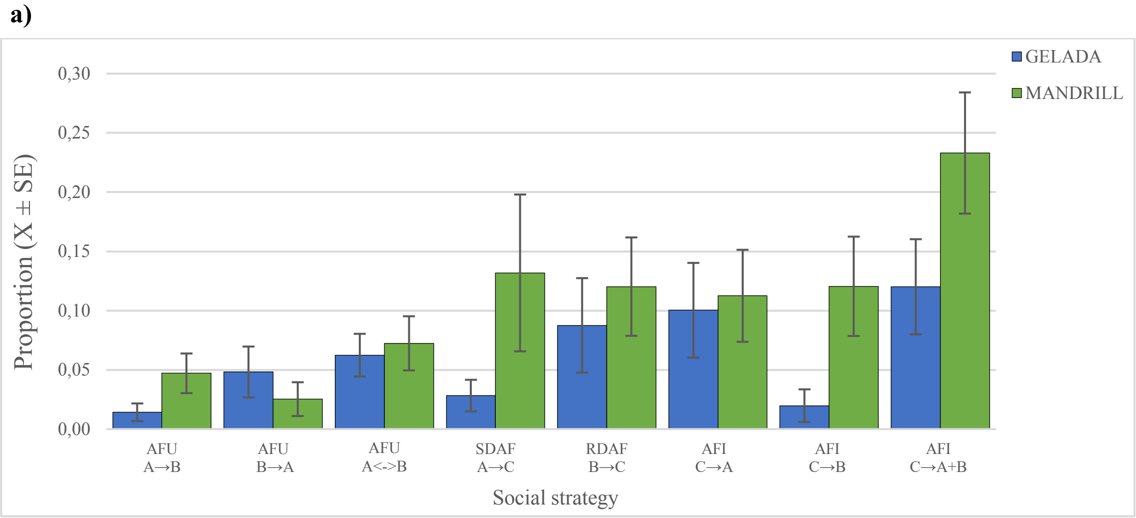
**Table 4.5** Ratios of social (aggressive and affiliative) strategies exhibited by geladas *versus* mandrills in each context (conflict and post-conflict) *

| | **Conflict** | | **Post-conflict** | |
|---|---|---|---|---|
| **Strategy** | **Geladas** | **Mandrills** | **Geladas** | **Mandrills** |
| CAG | **1.95** | | **In geladas only** | |
| RAG | 0.55 | | **1.12** | |
| SDAG | **3.04** | | **2.95** | |
| RDAG | **1.60** | | 0.60 | |
| AGI$_{A}$ | **8.55** | | **1.37** | |
| AGI$_{B}$ | 0.76 | | 0.09 | |
| AGI$_{A+B}$ | **1.56** | | 0.55 | |
| AFU$_{A}$ | 0.30 | | **11.06** | |
| AFU$_{B}$ | **1.90** | | **1.61** | |
| AFU$_{A+B}$ | 0.86 | | **3.29** | |
| SDAF | 0.21 | | **1.20** | |
| RDAF | 0.72 | | 0.54 | |
| AFI$_{A}$ | 0.89 | | **1.83** | |
| AFI$_{B}$ | 0.16 | | **1.90** | |
| AFI$_{A+B}$ | 0.51 | | **1.87** | |

*AG: aggressive strategies; AF: affiliative strategies. Scores over 1 mean that geladas scored higher than mandrills (i.e., geladas > mandrills, in boldface); under 1 that mandrills scored higher than geladas (i.e., mandrills > geladas).

As for the affiliative strategies, there were only two comparisons that yielded statistically significant differences between the two species, and these occurred during post-conflicts: AFU$_{A}$ (geladas > mandrills, $z = -2.2$, $p = 0.03$) and AFU (geladas > mandrills, $z = -1.95$, $p = 0.05$). During conflicts, mandrills outperformed geladas in 7 of 8 affiliative measures (Fig. 4.10a; Table 4.5), although this pattern was reversed during post-conflicts, where geladas scored higher than mandrills in 7 of 8 affiliative measures (Fig. 4.10b; Table 4.5). The only affiliative strategy that mandrills used more often than geladas in both contexts was redirected affiliation (RDAF), whereas the one affiliative strategy that geladas used more frequently than mandrills in both contexts was initiation of affiliation by victims (AFU$_{B}$).

Finally, no statistically significant differences were found between the two species in the rates of the two self-directed behaviours analysed (Fig. 4.11).



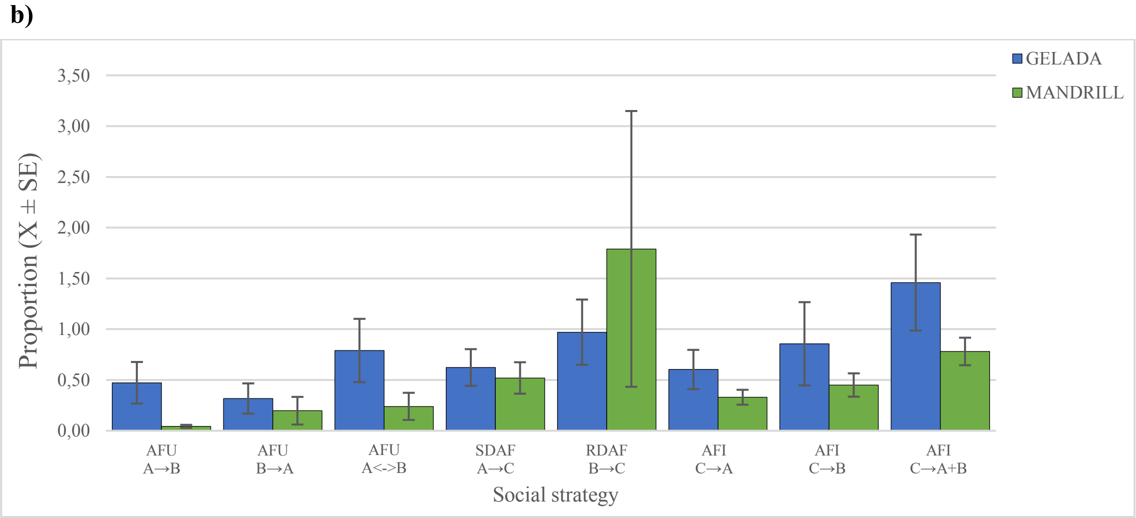


**Figure 4.10** Comparison of affiliative strategies used by geladas and mandrills (a) during conflicts, and (b) post-conflicts.

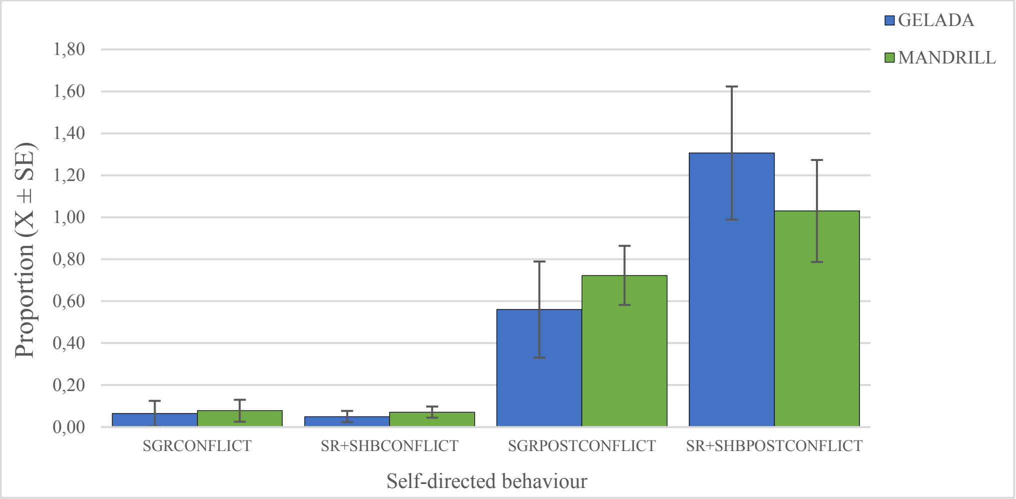


**Figure 4.11** Self-directed behaviours used by geladas and mandrills during conflicts *versus* post-conflicts.

## Discussion

The present study was aimed to provide a quantitative, comparative analysis of social (other-directed) behaviours and individual (self-directed) behavioural indicators of anxiety performed by geladas and mandrills in two contexts, during conflicts and during post-conflict observations. Our *first objective* was to test the Covariation Hypothesis (Thierry, 2000, 2004) by exploring the link between the variation in these two species' dominance or social style and, in our particular case, conflict resolution-related traits that are claimed to be correlated (see also, de Waal, 1989a, 1989b; de Waal and Luttrell, 1989). Unfortunately, neither geladas' nor mandrills' social styles have been clearly established, even though the former's social system has been thoroughly described in the wild (e.g., Dunbar, 1984, 1992; Kawai *et al.*, 1983; Snyder-Mackler *et al.*, 2012); in contrast, the social system of mandrills is still poorly known (Abernethy, White, and Wickings, 2002; Brockmeyer, *et al.*, 2015; Hongo, 2014). According to the Covariation Hypothesis, then, groups with steep, despotic or asymmetric (as opposed to shallow, egalitarian or symmetric) dominance hierarchies should score lower on post-conflict affiliation ('reconciliation') and counter-aggression (Balasubramaniam *et al.*, 2012; de Waal and Luttrell, 1989; Flack and de Waal, 2004; Thierry *et al.*, 2000, 2008; Thierry, 2000, 2004, 2007). And post-conflict affiliation should be initiated by victims more than by aggressors (de Waal, 1993; see Arnold, Fraser, and Aureli, 2011, and Colmenares, 2006, for reviews). The findings from the analysis presented here nicely fit predictions that follow from the Covariation Hypothesis. The dominance gradient was found to be steeper in mandrills than geladas (Chapter 3) and, as expected, post-conflict affiliation (AFU) was significantly more frequent in geladas than mandrills (79 % vs 24%, Fig. 4.10b) and gelada aggressors initiated such post-conflict affiliative interactions more often than mandrill aggressors ($AFU_A$, 47.2% vs 4.3%, Fig. 4.10b). However, in neither species was there any significant bias in who initiated the post-conflict affiliation (i.e., the aggressor or the victim; Figs. 4.4b and 4.8b). Also, in 47.5% of conflicts, geladas exhibited counter-aggression (CAG) *versus* only 24% in mandrills (Fig. 4.9a). In sum, as predicted by the Covariation Hypothesis, in this study and in both species, counter-aggression was positively related to post-conflict affiliation, that is, individuals and species that scored higher in counter-aggression tended to also score higher in post-conflict affiliation. And, when post-conflict affiliation was high, aggressors took more often the initiative than victims did in such post-conflict affiliative exchanges.

Swedell (1997) provided data on conciliatory tendencies in the gelada group she studied, but no information about rates of counter-aggression, which opponent initiated reconciliation, nor the study group' dominance style. Leone and Palagi (2010) also reported on the conciliatory tendency of their study geladas, and found that aggressors were more likely than victims to initiate post-conflict affiliation; however, they did not give information on counter-aggression rates or the group's dominance gradient. In the two studies of mandrill reconciliation published, data on conciliatory tendencies (Schino and Marini; Otovic *et al.*, 2014) and counter-aggression (Schino and Marini, 2011) were reported, however, they both focused on the types of behaviours used during post-conflict non-agonistic interactions between former opponents (e.g., contact *versus* non-contact), and no information was provided about who initiated post-conflict affiliative interactions nor the group's dominance gradient.

Our *second objective* was to test one prediction from the Relational Model of management of aggressive conflicts (de Waal and Aureli, 1997; de Waal, 2000a, 2000b). Although we did not use the traditional protocol of comparing levels of affiliation during post-conflict observations *versus* baseline observations or matched-control periods without aggression, our findings confirm that in both species the antagonists could and did switch their motivation very quickly from an aggressive mode (during the conflict) to an affiliative, or at least non-agonistic, mode (soon after the conflict had ended). In effect, in the aftermath of a conflict, instead of moving far away from each other (i.e., a 'repulsion' effect), aggressors and victims were attracted to each other and engaged in affiliative (or non-agonistic) interactions (i.e., a 'centripetal' effect). As we have already noted, this post-conflict friendly attraction between former opponents (AFU) was significantly more frequent in geladas than mandrills (i.e., 79 % vs 24%). Two studies of reconciliation, based on the traditional PC-MC comparison paradigm, have been conducted on captive groups of both species. Swedell (1997) and Leone and Palagi (2010) reported conciliatory tendencies of 45% (N = 11 individuals) and 23% (N = 18 individuals), respectively. And in the mandrill studies, the conciliatory tendencies reported were 12.1% (N = 14 individuals) and 23.5% (N = 9 individuals) (Schino and Marini, 2011; Otovic *et al.*, 2014). These results indicate that intra-specific variation in conciliatory tendencies is huge in geladas and mandrills, much as has been reported for many other primates (see Arnold *et al.*, 2011; Colmenares, 2006; Thierry, 2000, 2007, for reviews) and, therefore, even if species differences may still exist, local conditions defined in terms of demography and group structure or ecological conditions and competition regimes may produce considerable overlaps in the range of intra-specific variation.

Our *third objective* was concerned with the study of the extra-dyadic dimension of conflicts in the two species. We specifically looked at the percent of conflicts in which the initial dyadic interactions between the antagonists spread beyond the dyad and became polyadic (Colmenares and Rivero, 1986; Colmenares, 1996a). This 'polyadicity' could emerge out of two different paths with regards to the *direction* of the behaviours, from initial antagonists towards third-parties (*side*-directed actions by aggressors and *re*-directed actions by victims) or from third-parties towards former opponents (*interventions* targeting aggressors and *interventions* targeting victims). And these two paths could further be classified according to the *type* of behaviours used by the antagonists and by the third-parties. Thus, we have *side*-directed and *re*-directed *aggression* (SDAG and RDAG) and *affiliation* (SDAF and RDAF), on the one hand, and *aggressive* and *affiliative intervention* (AGI and AFI, respectively), on the other, which could be further divided according to the 'intervention direction' (de Waal, 1978a, 1978b; Petit and Thierry, 1994, 2000), that is, directed towards aggressors or towards victims ($AGI_A$ and $AGI_B$, and $AFI_A$ and $AFI_B$, respectively).

In geladas, in 23.6% and 27% of conflicts, aggressors and victims directed aggressive behaviours towards bystanders, respectively (SDAG and RDAG, Fig. 4.9a). In mandrills, aggressors and victims also aggressively targeted bystanders, although their scores were significantly lower (SDAG: 7.8%; RDAG: 16.8%, Fig. 4.9a). Once more again, gelada aggressors and victims behaved more alike than mandrill aggressors and victims did in the use of aggressive behaviours directed at non-involved third-parties. We have no comparable published data on side-directed and re-directed aggression in geladas or mandrills. In Watts, Colmenares, and Arnold (2000) review of redirected aggression and other aggressive interactions between opponents and third-parties in primates, the authors claimed that redirected aggression was probably an alternative to counter-aggression, that is, redirection should be more likely to arise when counter-aggression is unlikely. In the present study, however, geladas were more active than mandrills both in redirected aggression (RDAG) as well as in counter-aggression (CAG).

Schino and Marini (2014) studied redirected aggression (towards the aggressor's kin) and counter-aggression in mandrills and hypothesized that both could be regarded as forms of indirect and direct retaliatory behaviour or punishment (cf. Clutton-Brock and Parker, 1995), respectively, in that they might reduce the probability of re-aggression by the aggressor. Their analyses revealed that kin-oriented redirected aggression did function as punishment as it certainly reduced the risk of renewed aggression. In the present study we did not specifically addressed this hypothesis, however, as already mentioned, we found an inverse relation between the two forms of aggression. Thus, geladas used RAG *less often* and RDAG *more often* than mandrills (RAG and RDAG; Fig. 4.9a). Interestingly, and rather surprisingly, nobody has ever described and analysed the other form of aggressive behaviour directed at third-parties, in this case by aggressors, not victims, that we have labelled side-directed aggression (SDAG). In our study, 23.6% of gelada conflicts *versus* only 7.7% of mandrill conflicts gave rise to this form of triadic aggression (Fig. 4.9a).

Antagonist-initiated forms of affiliation with third-parties include side-directed and redirected affiliation (SDAF and RDAF). In both species, victims were more prone than aggressors to initiate affiliation with third-parties, although overall this category was much used by both antagonists (RDAF *versus* SDAF; geladas: 97% *vs* 62%; mandrills: 171% *vs* 52%, respectively; Fig. 4.10b). The functions of antagonist-initiated affiliation with third-parties can be manifold, and clues about specific functions can be obtained by looking at the identity of the targeted third-party (high- or low-ranking individual, own *versus* the other antagonist' ally or kin) and the effects of such affiliative interactions on the conflict's outcome, for example, the risk of re-aggression, the probability of third-party aggressive or affiliative (favourable or disfavourable) interventions, the antagonists' levels of anxiety (Das, 2000; Aureli *et al.*, 2012). We did not analyse that information in our study, but it is noteworthy that in both species the rates of third-party affiliative and, to a lesser extent, aggressive interventions were remarkably high (Figs, 4.10b and 4.9a, respectively). In the mandrill group, victim-initiated redirected affiliation was high and third-party aggressive intervention against victims was also relatively more elevated than against aggressors. This suggests a self-protection or appeasement function for redirected affiliation. It is also interesting, and rather puzzling, to note that in the first quantitative study of antagonist-initiated affiliation de Waal and Yoshihara (1983) reported that it was aggressors, not victims, who actually exhibited the highest levels of side-directed affiliation (what they termed 'redirected affection'), and this occurred in rhesus macaques, which is the icon species of a despotic dominance style (de Waal, 1989a, 1989b; de Waal and Luttrell, 1989; Thierry, 2000, 2004; Thierry *et al.*, 2008).

Aggressive interventions by third-parties (AGI) were more common in geladas than mandrills (75% *vs* 48%, respectively, Fig. 4.9a) and the former were also more likely than mandrills to support victims ($AGI_A$, 42.6% *vs* 5%, respectively, Fig. 4.9a). Nevertheless, in both species there was also an important proportion of conflicts in which third-parties aggressively intervened on behalf of aggressors ($AGI_B$, 32.8% *vs* 43%, respectively, Fig. 4.9a). In a study of third-party aggressive interventions in a group of geladas, Pallante *et al.* (2016) found that victims were more often supported than aggressors ($AGI_A > AGI_B$, in our notation) and that such interventions on behalf of victims were effective in reducing the occurrence of re-aggression, not only between the former opponents, but also in the group as a whole. The study of aggressive interventions and, especially, of its role in controlling the levels of intra-group aggression in different species has been a key topic in social ethology and comparative psychology of social relationships (Bernstein, 2011; Boehm, 1981, 1994; Chapais, 1995; Harcourt and de Waal, 1992; van Schaik, 2016; Watts *et al.*, 2000).

Ongoing dyadic (or already polyadic) conflicts often trigger the affiliative intervention of third-parties (Arnold *et al.*, 2011; Aureli *et al.*, 2012; Das, 2000; Fraser *et al.*, 2009). In our study, affiliative interventions were very frequent during post-conflicts (AFI: 145% and 78% in geladas and mandrills, respectively; Fig. 4.10b), and they targeted aggressors as often as victims. The only noticeable (but still non-significant) result was that, during conflicts, mandrill third-parties were more active than gelada third-parties in affiliating with victims ($AFI_B$, 12% *versus* 2%, respectively, Fig. 4.10a).

There is abundant behavioural and pharmacological evidence that individuals do experience high levels of anxiety after conflicts, as shown by the rise in the rate of a number of anxiety-related behavioural indicators, particularly self-directed behaviours, including body-shake, self-scratch, and self-groom, that conflict participants exhibit during post-conflict observations (Maestripieri, Schino, Aureli, and Troisi, 1992; Schino, Troisi, Perretta, and Monaco, 1991; Schino, Rosati, Geminiani, and Aureli, 2007; Troisi, 2002). In the present study we confirmed that the self-directed behaviours analysed increased significantly during post-conflicts in both species (Fig. 4.11).

This study adds new empirical observations on strategies of conflict-resolution in two species that have received scant attention in this research area. It also expands what we know about conflict management strategies in general by empirically documenting (a) an inverse relation between dominance gradient and levels of reconciliation and counter-aggression (Covariation hypothesis); (b) a quick shift from an agonistic mode to an affiliative one (Relational Model); (c) a huge amount of polyadic interactions with frequent exchanges, in both directions, of aggressive and affiliative behaviours between antagonists and third-parties; and, finally, (d) the occurrence of high levels of anxiety-related self-directed behaviours during the aftermath of an agonistic conflict.

# CHAPTER 5

# General Discussion and Conclusions

## Discussion

The research reported here was aimed to probe some of the mechanisms that provide a scaffold for the sociality and prosociality (cooperation) so characteristic of primates (and other animals). The sociality of primates is bonded and social bonds need to be serviced if they are to enhance the individuals' welfare and biological fitness (Dunbar and Shultz, 2010; Kummer, 1978; Seyfarth and Cheney, 2012; Silk, 2012). It is now well-established that the primates' social systems are fully described when adequate attention is paid to all of its four components, that is, the grouping pattern, the demographic processes, the mating (and parenting) systems, and the group structure (Kappeler and van Schaik, 2002, Kappeler *et al.,* 2013; Nystrom and Ashmore, 2008; Fuentes, 2011; Schülke & Ostner, 2012; Koenig *et al.* 2013). And it is also rather well established that a fully understanding of group structure (*sensu* Hinde, 1976) should include the analysis of four major categories of behaviour, aggression, affiliation, reconciliation and cooperation (Colmenares, 2015).

Now, raw data never speak for themselves. Conceptual and theoretical frameworks are necessary for asking theoretically relevant research questions, for spelling out the assumptions and predictions that follow, for guiding the design of protocols that enable the collection and analysis of pertinent data and, ultimately, for assessing the results obtained in light of current or revised theories. Contemporary research on primate social systems emphasizes the need for integrating socioecological theory, evolutionary history and life-history theory (see Chapman and Rothman, 2009; Clutton-Brock and Janson, 2012; Di Fiore and Rendall, 1994; Fuentes, 2011; Kappeler *et al.,* 2013; Koenig *et al.,* 2013; Kutsukake, 2009; Parga and Overdorff, 2011; Schradin, 2013; Schülke and Ostner, 2012; Shultz, Opie and Atkinson, 2011; Thierry, 2008, 2013; van Schaik, 2016, van Schaik and Isler, 2012, for recent reviews). Contemporary theory does acknowledge that a full understanding of the proximate and ultimate causes of variation in primate social systems requires an eclectic approach that judiciously combines correlational and experimental studies.

The present research was aimed to study sociality and prosociality in two groups of African papionins, geladas (*Theropithecus gelada*) and mandrills (*Mandrillus sphinx*), housed in rather similarly naturalized, sized and vegetated enclosures in captivity. Their ecological setting was benign in that the groups were food-provisioned and predation free. We set out (a) to analyse the two groups' activity time budgets, (b) to carry out a fine-grained study of the individuals' socio-spatial behaviour, (c) to test the prediction of the biological market theory that a group's dominance gradient will influence the patterns of reciprocity and interchange of grooming and prosocial behaviour (i.e., punishment), (d) to test the prediction of the Covariation hypothesis that the patterns of conflict management tend to be intercorrelated and are related to the group's dominance style and hierarchy steepness, and (e) to test the prediction of the Relational model that individuals that have participated in an agonistic encounter are likely to promptly switch their motivation from an aggressive "mode" to an affiliative "mode" and to engage in affiliative behaviours right after the conflict has ended.

### *Activity budgets*

Although the two study groups were in a benign ecological setting in that there was no predation pressure and individuals were food-provisioned, their time budget decisions were found to match closely those that have been reported for ecologically stressed wild populations of gelada and *Papio* baboons (Dunbar, 1992a, 1992b). Geladas kept high levels of *foraging* time, lowered *moving* time, and kept relatively high levels of *social* time. Mandrills exhibited high levels of *foraging* and *moving* times, but, in contrast to geladas, their *resting* time was far higher than their *social* time. These findings add to the lively ongoing debate as to how groups should respond to stressful *versus* relaxed ecological conditions (e.g., human food-provisioning). When individuals increase their *foraging* time in response to more demanding energy requirements (e.g., when mothers are lactating, see Altmann, 1980; Dunbar and Dunbar, 1988), when food is more dispersed and scarce, or when group size increases, they must take it out of *resting* time *versus social* time (Dunbar, 1992b; Bronikowski and Altmann, 1996). Also, when wild populations feed on human derived food resources (e.g., garbage dumps or crops) and, as a consequence, their *foraging* time budget relaxes, individuals have been reported to increase *resting* rather than *social* time (Altmann and Muruthi, 1988; Bronikowski and Altmann, 1996; see also Jaman and Huffman, 2008, 2013).

In both groups, affiliative behaviour was by far the category of social activity that the individuals spent more time in. And play was next. Aggressive behaviour accounted for a very tiny proportion of the individuals' time budgets (i.e., about 1%-1.3%). These findings mirror those reported for wild populations (Sussman and Garber, 2011). It seems that the higher social density that the two groups experienced as a consequence of their captivity conditions did not increase their aggressive behaviour compared to their wild counterparts (see de Waal, 1989; de Waal *et al.,* 2000; Judge, 2000). The results from this study thus lend further support to the idea that the construct 'captivity' is largely meaningless when one wants to account for the behaviour of primates housed in captive settings (Colmenares, 2006).

### *Socio-spatial behaviour*

The rather fine-grained analysis of the socio-spatial behaviour of the individuals in the two study groups, assessed through two indices, namely, *sociality* (i.e., being accompanied or alone) and *gregariousness* (i.e., if accompanied, how many neighbours you were with), and at four different social distance categories, from physical contact up to within four meters, yielded two main results. First, within a radius of up to two arms' reach, individuals spent most of the time alone. Second, when they were accompanied, they tended to be in duos or trios up to a distance of two arms' reach, and beyond that social distance they were hardly found in quartets. This underscores the nature of the bondedness of primate sociality (Dunbar and Shultz, 2010). Even though, fear to predators is a potent and probably primary proximate factor that makes individuals of many species more likely to aggregate (Alexander, 1974; van Schaik, 1983; Dunbar, 1988), it appears that natural selection has favoured the evolution of psychological mechanisms such as emotional attachments that foster bonding and attraction to conspecifics (Mason, 1968, 1976, 1997; Mendoza, Reeder and Mason, 2002), even in the absence of predators, which is the case in captive settings. It is also intriguing to realize that the grouping patterns and overall cohesion of primate groups might be largely sustained by the assembly of a rather dyadic or triadic template of proximity relations.

### *Dominance gradient, reciprocity and interchange of services*

The dominance hierarchy of the mandrill group was found to be steeper than that of the gelada group. This difference in the two groups' dominance gradients allowed the study of the impact of variation in the power differentials between individuals on the patterns of reciprocity and interchange of aggression, grooming and punishment. Prior work has documented the existence of a relation between the steepness of a group's hierarchy and the pattern of reciprocity in grooming and of interchange of grooming for agonistic support (e.g., Barrett and Henzi, 2001, 2006; Hemelrijk and Puga-Gonzalez, 2012). The present study expanded this by adding reciprocity of aggression and of punishment, and interchange of aggression for grooming, of aggression for punishment, and of grooming for punishment. In the analyses punishment was broken down into its two components, when the third-parties' punishment was directed at aggressors (i.e., they helped the victims) and when they targeted victims (i.e., they joined or supported aggressors).

The approach adopted in this study was based on the biological market theory (Hammerstein and Noë, 2016), was correlational, and was performed at a group level (Hemelrijk, 1990a, 1990b). This meant that we treated the groups as 'biological markets', where individuals traded behaviours regarded as 'services', 'commodities' or 'goods', and spelled out and tested several assumptions and predictions of biological market theory by running correlations between actor matrices and receiver matrices (Hemelrijk, 1990a, 1990b, Hemelrik and Ek, 1991; Hemelrijk and Puga-Gonzalez, 2012; Mitani, 2006; Newton-Fisher and Lee, 2011; Kaburu and Newton-Fisher, 2015; Watts, 1997, 2002). In the analyses of reciprocity and interchange there were two matrix variables that were statistically controlled, namely, dominance rank and proximity, as they are known to correlate with variables such as the ones tackled in the present study and, therefore, can identify potentially spurious (false) cases of reciprocity and interchange (de Waal and Luttrell, 1988; de Waal and Brosnan, 2006; Hemelrijk, 1990a, 1990b, Hemelrijk and Ek, 1991; Hemelrijk and Puga-Gonzalez, 2012; Mitani, 2006; Watts, 2002).

As expected, dominance rank was found to generally predict the (uni)directionality of aggression and punishment; however, it turned out to be a rather poor predictor of the direction of grooming, a behaviour commonly used to service social bonds and cooperating partnerships (Schino and Aureli, 2008a, 2008b for reviews). The latter finding is especially relevant as two key assumptions of biological market theory (Barrett and Henzi, 2001, 2006), and of its predecessor, the Seyfarth's (1977, 1980) model of grooming, is that low-ranking individuals are expected to be more active groomers than high-rankers (i.e., they use grooming to trade for agonistic support received) and that grooming is expected to be directed up the hierarchy (i.e., agonistic support is a service offered or 'sold' by high-rankers in exchange for grooming).

Grooming was massively positively associated with time spent in proximity in both species, a finding commonly reported in the primate literature. This association was much less strong, although not inexistent altogether, for aggression or punishment. Thus, in mandrills some of the measures of aggression and punishment tended to score higher with group mates that were frequent neighbours at some of the distance categories analysed.

As expected, the unidirectionality of aggression was stronger in the group with greater dominance gradient. And, as expected too, victim punishment (i.e., aggressive interventions against victims) was found to be strongly unidirectional in the mandrill group, where power differentials were rather steep. In contrast, in the more egalitarian geladas aggressor-punishment (i.e., aggressive interventions against aggressors) was found to be reciprocal. This finding is consistent with the prediction that punishment (or aggressive interventions generally) are more likely to elicit counter-aggression in social groups with shallow dominance hierarchies (de Waal and Luttrell, 1988; de Waal and Brosnan, 2006).

Interestingly, although aggressive interventions by third-parties tended to go down the hierarchy in both groups, in the gelada group, where third-parties sometimes protected the victim against his or her higher-ranking aggressor, 'bridging' alliances (Chapais, 1995) were also recorded. This lends support to the hypothesis that aggressor punishment can have a pacifying function as it can stop ongoing dyadic agonistic encounters and can contribute to smooth power differentials in the group (Boehm, 1981; Kaplan, 1987; Pallante *et al.,* 2016; van Rohr *et al.,* 2012; Watts *et al.,* 2000).

Contrary to expectations (e.g., Barrett *et al.,* 2002; Henzi *et al.,* 2003), grooming was found to be reciprocated regardless of variation in dominance gradient. In fact, this reciprocity was independent of proximity and, as already pointed out, dominance rank too. This pattern is very robust as it has been reported to occur in both female-bonded (see Hemelrijk and Puga-Gonzalez, 2012; Schino and Aureli, 2008a, 2008b for reviews; see also Schino and Pellegrini, 2009 in mandrills) and in male-bonded (chimpanzees: Mitani, 2006; Watts, 2002; Newton-Fisher and Lee, 2011; Kaburu and Newton-Fisher, 2015) groups. In our study this pattern emerged even though the analyses of grooming at group level combined same- and cross-sex dyads.

In both study groups a weak pattern of interchange of aggression for grooming was detected, however, since the study was correlational it is difficult to tell which was more likely to cause which (see also Schino, Ventura, and Troisi, 2005). Thus, grooming could be used to appease aggressors and reduce the probability of renewed aggression, to reconcile after a fight, or both (Arnold *et al*., 2011; Aureli *et al.,* 2012). It could also be the case that many instances of aggression directed at frequent groomers were actually instances of side-directed or re-directed aggression, which might be targets at individuals they had a bond with. To test these hypotheses an analysis of short-term contingency between aggression and grooming is required (Cheney and Seyfarth, 2012; Hemelrijk, 1994; Schino *et al.,* 2005; Schino and Aureli, 2009; Schino and Alessandrini, 2015).

As expected, in the group with the shallow dominance hierarchy there was interchange of aggression and aggressor-punishment (see above), whereas in the other group with a more despotic hierarchy this pattern turned unidirectional when punisher-victim target dyads were analysed. The underlying principle is the same, when power differentials are small, like between punishers and aggressor targets in the egalitarian geladas, interchange is expected to arise. In contrast, the opposite pattern of unidirectionality is expected to surface in dyads of punishers and victim targets in the more despotic mandrill group.

Although the results obtained generally supported most of the tested assumptions and predictions derived from the biological market approach adopted here, however, there were two core predictions that failed to be supported. Contrary to expectations, there was reciprocity of grooming regardless of variation in dominance gradient. And, although, as expected, there was a negative (unidirectional) interchange of grooming for punishment in the group with greater dominance gradient, the correlation was only marginally significant. These findings along many others reported in the literature (see Hemelrijk and Puga-Gonzalez, 2012; Schino and Aureli, 2008a, 2008b for reviews) highlight the importance of partner choice in understanding the way individuals service their social bonds (friendships and alliances) in a social niche where multiple partners are potentially available and actively engaged in outbidding competition (Noë and Hammerstein, 1994, 1995).

### *Dominance style and patterns of conflict-management*

The findings from this study supported the covariation hypothesis (Thierry, 2000, 2004), as it was found that the group with a more egalitarian dominance style (i.e., that of geladas) scored higher in counter-aggression, post-conflict affiliation, and initiation of reconciliation by aggressors than the group with a more despotic dominance style (i.e., that of mandrills).

The study also provided further support to the prediction of the relational model of aggression (de Waal and Aureli, 1997; de Waal, 2000a, 2000b), as the rates of affiliative behaviour were observed to increase markedly soon after the aggressive conflicts had ended. In other words, there was the predicted quick switch in the antagonists' motivation, from aggression to affiliation.

### *Species differences*

Geladas and mandrills differed in many of the behavioural measures analysed in this study. Those having to do with the patterns of unidirectionality, reciprocity and interchange have already been mentioned (see above), however, there were a few others that should be evaluated now. Geladas were more sociable (in terms of the budget allocated to social time and in terms of the time spent in the company of others *versus* alone) and gregarious (in terms of the time spent with one or two neighbours at most of the social distance categories analysed) than mandrills (chapter 2).

Geladas were more actively engaged in affiliative (grooming) interactions and performed fewer dominance and aggressive behaviours than mandrills, and were more likely than mandrills to intervene on behalf of victims (chapter 3). Geladas were more likely than mandrills to deploy counter-aggression, to engage in post-conflict affiliation, and for aggressors to initiate post-conflict affiliation (chapter 4). These findings fit well with predictions that follow from the biological markets and the covariation hypotheses.

### *Limitations of this study*

Although the methods of study adopted in this research, that is, correlational (at group level), cross-sectional, and comparative with just one group per species, were not different from those considered standard in this field, however, it is fair to acknowledge that some of the conclusions drawn from this study should only be regarded with caution, even if they are supported by previous work. The small size of one of the groups, the lack of (short-term) contingency data, and the lack of matched-control observations of conflicts were the most important limitations of this study.

With regard to the issue of species differences, for example, it should be stated that at this stage it is difficult to tell the extent to which the observed differences between geladas and mandrills can be accounted for by species-specific differences in social dispositions (i.e., phylogenetic constraints), demographic factors (i.e., current demographic structure), ontogenetic and experiential factors (i.e., the rearing history of the incumbent individuals) or even the quality of the social relationships (e.g., how long they had known one another), as all of them are known to shape the individuals' social interactions, their social relationships and, ultimately, their group structure (Hinde, 1976, 1983; Mason, 1979).

## Conclusions

1. Despite their living in an ecological setting free of predators and food-provisioned, the two study groups' activity budgets fell well within the range of variation of *activity budgets* that have been described for wild populations of gelada and *Papio* baboons that are ecologically stressed. This finding raises the question as to why in the highly benevolent ecological conditions that the two groups faced in captivity the individuals' time budgeting decisions appeared to be so resilient.

2. Although the two groups' overall activity budgets were similar, they were not identical. Both geladas and mandrills kept high levels of *foraging* time, however, the former kept higher levels of *social* than *moving* time, and the latter scored higher in *resting* than *social* time.

3. In both groups, the time spent in *affiliative behaviour* was far greater than that spent in *aggression*. This pattern has also been reported to occur in wild populations. These results lend support to the view that the relation between captivity and behaviour is far from simple. Within certain limits of ecological variation and in strongly socially evolved species, individuals appear to be more sensitive to the social and demographic characteristics of the socio-ecological niches they encounter in captivity than to other variables typically associated with captive settings.

4. The individuals from the two study groups were found to spend most of the time alone, i.e., without neighbours, within a radius of two arms' reach. This rather weak *sociality* was shared by both species; none the less, geladas scored higher than mandrills in sociality at all social distance categories analysed.

5. In both groups, the individuals' *gregariousness*, i.e., the number of neighbours found at the various categories of social distance, was found to be rather meagre. When they were accompanied within the radius of two arms' reach, they were hardly found with more than two partners. And at the farthest distance this pattern was not much different, either. As with sociality, geladas were also more gregarious than mandrills. This socio-spatial organization where individuals are mainly arranged in duos or trios is intriguing and raises important issues with regard to the nature of group cohesion and its behavioural, psychological, and socio-ecological underpinnings.

6. The dominance hierarchy of the mandrill group was steeper than that of the geladas'. Contrary to the predictions of the biological market theory, grooming was reciprocally exchanged regardless of variation in dominance gradient. In line with the expectations, there was a negative (unidirectional) interchange of grooming for punishment in the group with greater dominance gradient; however, this correlation was only marginally significant.

7. Dominance rank was generally found to be a good predictor of the distribution of dyadic and triadic aggression; however, it did not predict the distribution of affiliative (grooming) measures. This rank independency of grooming could explain why it was reciprocated for itself rather than interchanged for agonistic support or, in our study, the avoidance of punishment.

8. Grooming partnerships were found to be strongly related to time in spatial association (i.e., proximity partnerships). However, in several cases, the patterns of reciprocity and interchange found were independent of proximity. That is, individuals were found to give relatively more often of a given behaviour to those from whom they received relatively more often of that same (in reciprocity) or another behaviour (in interchange) in return. This meant that reciprocity or interchange was genuine and not a by-product of proximity.

9. As expected, aggression and victim-punishment, where the power differentials between the punishers and the targets were more elevated, were both unidirectional, a pattern that was stronger in the group with steeper dominance hierarchy. And, as expected, aggressor punishment was reciprocal in the group with smoother dominance gradient.

10. Aggressive interventions by third-parties tended to go down the hierarchy, which implies that they minimized risks of retaliation. However, in the more egalitarian group of geladas, some of the interventions were not 'conservative', but 'bridging', which means that interveners supported the lowest-ranking individual (i.e., the victim) against the middle-ranking opponent (i.e., the aggressor).

11. Aggression was interchanged for grooming. Since the study did not analyse short-term contingency between the behaviours given and received it is not possible to establish if grooming was used to appease current aggressors' renewed aggression or/and to service a partnership which might buffer against future potential aggressions from the groomee. Neither can we determine if the aggressors' aggressive behaviours were actually instances of side-directed or redirected aggression against partners they were bonded to.

12. The test of the covariation hypothesis confirmed that the rates of counter-aggression and post-conflict affiliation, and the initiation of post-conflict affiliation by aggressors were intercorrelated and were associated with the more egalitarian dominance style of the gelada group.

13. The study provided support for the prediction of the relational model that the rates of affiliative behaviour were observed to increase markedly soon after the aggressive conflicts had ended. In other words, there was the predicted quick switch in the antagonists' motivation, from aggression to affiliation.

14. Although the methods of study adopted in this research, that is, correlational (at group level), cross-sectional, and comparative with just one group per species, were comparable to those that are considered standard in this field, however, it is fair to acknowledge that some of the conclusions drawn from this study can only be regarded as tentative, even if they are supported by previous work. The small size of one of the groups, the lack of (short-term) contingency data, and the lack of matched-control observations of conflicts were the most important limitations of this study.

15. The findings from this study add to the growing contemporary perspective on the bonded nature of primate sociality, where individuals are regarded as 'traders' that actively budget their social time to service their welfare- and fitness-enhancing bonds and cooperative partnerships. They show that individuals compete and cooperate through the reciprocal or unidirectional exchange of services (grooming and support) and the repairing of bonds disrupted by aggression through post-conflict friendly exchanges. The study also highlights the importance of demographic constraints that lead to fast changes in the biological market (e.g., dominance gradients) and of phylogenetic constraints that cause the evolution of correlated traits (e.g., dominance styles). Finally, this research is a contribution to the notion that the strategies of social behaviour seen in social groups reflect the operation of processes of partner choice, where individuals engage in outbidding competition and switch partnerships when the cost/benefit ratio is no longer balanced.

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