The season for peace: reconciliation in a despotic species (*Lemur catta*)

However despotic a social group may be, managing conflicts of interest is crucial to preserve group living benefits, mainly based on cooperation. In fact, in despotic groups post-conflict management via reconciliation (the first post-conflict reunion between former opponents) can occur, even if at variable levels. In the despotic *Lemur catta* reconciliation was reported in one out of four captive groups. We used this species as a model to understand what variables influence the occurrence of the reconciliation in despotic groups. We analyzed 2339 PC-MC collected on eight groups (five in the Berenty forest, Madagascar; three hosted at the Pistoia Zoo, Italy). Since Lemur catta is characterized by rigid female dominance but show female-female coalitionary support, we expected to find reconciliation in the wild, other than in captivity. Consistently, we found the phenomenon to be present in one captive group and two wild groups, thus providing the first evidence of the presence of reconciliation in wild *Lemur catta*. Being this species a seasonal breeder (with mating occurring once a year), we expected that the season more than other variables (wild/captivity setting, rank, or individual features) would influence reconciliation levels. Via GLMM we found that the season was indeed the only variable significantly explaining reconciliation rates, lowest during mating and highest during the pregnancy period. We posit that reconciliation can be present in despotic species but not when the advantages of intra-group cooperation are annihilated by competition, as it occurs in seasonal breeders when reproduction is at stake. By comparing our results with literature, we conclude that in despotic social groups in which coalitions are observed, the right question is not *if* but *when* reconciliation can be present.

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THE SEASON FOR PEACE: RECONCILIATION IN A DESPOTIC SPECIES (*Lemur catta*)

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INTRODUCTION

Managing conflicts of interest is crucial to preserve group living benefits, also in despotic societies. In these kind of societies, integrity is usually maintained through "negative peace" (*sensu* Galtung, 1969) because the absence of violence spreading is often forcibly controlled by dominants. Yet, in humans and other social mammals dominant individuals or subgroups may need the support of others to obtain resources and maintain the *status quo* (Bygott, Bertram & Hanby, 1979; Clutton-Brock, 1998; Duffy, Wrangham & Silk, 2007; Cordoni & Palagi, 2008; Dovidio, Saguy & Shnabel, 2009; Snyder-Mackler, Alberts & Bergman, 2012). Consequently, strategies of mutual support – other than competition for dominance and resources - must be enabled, such as cooperative breeding, cooperative hunting, and cooperation in between-group conflicts (e.g. see Boesch, 1994; Smith et al., 2010b; Soma & Koyama, 2013; Baan et al., 2014). Reconciliation or peace-making, defined as the first post-conflict affinitive contact between former opponents, is one of the main mechanisms to manage conflicts (de Waal, 2004). The phenomenon is largely present in social animals, spanning birds (ravens, *Corvus corax*: Fraser & Bugnyar, 2011) and mammals (e.g., domestic goats, *Capra hircus*: Schino, 1998; dolphins, *Tursiups troncatus*: Weaver, 2003; domestic dogs, *Canis lupus familiaris*: Cools, van Hout & Nelissen, 2008; horses, *Equus caballus*: Cozzi et al., 2010; red-necked wallabies, *Macropus rufogriseus*: Cordoni & Norscia 2014), including human and non human primates (*Homo sapiens*: Fujisawa, Kutsukake & Hasegawa, 2005; chimpanzees, *Pan troglodytes*: de Waal & van Roosmalen, 1979; Arnold & Whiten 2001; bonobos, *Pan paniscus*: Palagi, Paoli & Borgognini Tarli, 2004; wild macaques, *Macaca* spp.: Aureli, 1992; Cooper, Aureli & Singh, 2007; captive guereza, *Colobus guereza*: Björnsdotter, Larsson, & Ljungberg, 2000; captive squirrel monkeys, *Saimiri sciureus*: Pereira, Schill & Charles, 2000; captive white-faced capuchins, *Cebus capucinus*: Leca et al., 2002).

By restoring the relationship between former opponents (de Waal, 1986; Cords 1992; Kappeler & van Schaik, 1992; Cords & Thurnheer, 1993; Aureli & de Waal, 2000; Demaria & Thierry, 2001; Wittig & Boesch, 2005; Aureli & Schaffner, 2006), reducing the probability of further fights (Aureli, van Schaik & van Hooff, 1989; Aureli & van Schaik ,1991; Cords, 1992; Watts, 1995a; Watts, 1995b; Koyama, 2001; Kutsukake & Castles, 2001; Palagi, Chiarugi & Cordoni, 2008; Norscia & Palagi, 2011) and/or reducing anxiety in the victim (Castles & Whiten 1998; Das, Penke & van Hooff, 1998; Aureli & Smucny, 2000; Arnold & Whiten, 2001; Butovskaya et al. 2005; Palagi & Norscia, 2011), reconciliation is crucial to preserve social unity by the disruption caused by conflicts that spread across the group without any form of control. Therefore, reconciliation is expected to be present, also in despotic societies, any time that it is valuable for the group members (including dominants) to maintain the alliances that allow group survival, thus preserving the benefits of group living. Indeed, reconciliation has been found also in despotic species (e.g., spotted hyenas, *Crocuta crocuta*: Wahaj, Guse & Holekamp, 2001; wolves, *Canis lupus lupus*: Cordoni & Palagi, 2008; wild mountain and captive lowland gorillas, *Gorilla beringei* and *Gorilla gorilla*: Watts 1995a; Watts 1995b; Cordoni, Palagi & Borgognini Tarli, 2008; Japanese macaques, *Macaca fuscata*: Chaffin, Friedlen & de Waal, 1995; wild chacma baboons, *Papio ursinus*: Cheney, Seyfarth & Silk, 1995; captive patas monkeys, *Erythrocebus patas*: York & Rowell, 1988).

The linkage between reconciliation and inter-individual tolerance has been qualitatively examined in humans, with friendly peacemaking being favored by minimal authority (Fry, 2012) and quantitatively assessed in macaques, with tolerant species showing higher reconciliation levels than despotic species (Tonkean macaque, *Macaca tonkeana*; Palagi et al., 2014; Demaria & Thierry, 2001; Petit & Thierry, 1994; Thierry, 1985a; Thierry 1985b; crested macaques, *Macaca nigra*: Petit, Abegg & Thierry, 1997; Japanese macaques, *Macaca fuscata*: Chaffin, Friedlen & de Waal, 1995). The same linkage has been hypothesized in strepsirrhine primates

(Kappeler, 1993), in which reconciliation was indeed found in tolerant species (captive *Eulemur rufus:* Kappeler, 1993; Roeder, Fornasieri & Gosset, 2002; wild *Propithecus verreauxi*: Palagi, Antonacci & Norscia, 2008; wild *Eulemur rufusxcollaris:* Norscia & Palagi, 2011) but not in the despotic *Eulemur macaco* (in captivity, Roeder, Fornasieri & Gosset, 2002). The ability of despotic *Lemur catta* to reconcile has been difficult to prove. In fact, the phenomenon was found in one but not in three other captive troops in which reconciliation was studied (Kappeler, 1993; Palagi, Paoli & Borgognini-Tarli, 2005). We posit that the puzzling situation observed in *Lemur catta* is related to the fact that in despotic societies, conflict management strategies are difficult to be accommodated into group dynamics, which are mainly shaped by the control of the dominant. However, there are times when individuals can invest in conflict management because the costs of conflicts outweigh their benefits (Baan et al., 2014). Based on this main assumption, we used the primate *Lemur catta* as a model species to investigate if and when reconciliation could be found in different despotic groups. As a primate species belonging to the group (strepsirrhines) that diverged from the human primate line some 60 million years ago (Fleagle 2013), *Lemur catta* also offers the possibility to make inferences about the biological roots of peace-making dynamics found in human and non human primates. For this investigation, we analyzed the data collected on the model species both in the wild and in captivity across more than a decade to verify the following predictions:

Prediction 1

Similar to wolves and hyenas (Frank, 1986; Fentress et al., 1987; Cordoni & Palagi, 2008), *Lemur catta* is characterized by rigid hierarchy and high competition levels (Jolly, 1966; Sussman & Richard, 1974; Palagi, Telara & Borgognini Tarli, 2003; Palagi, Telara & Borgognini Tarli, 2004; Sclafani et al., 2012;). Analogously to ring-tailed lemur troops, packs (in the case of wolves; Messier, 1985) or clans (in the case of hyenas: Henschel & Skinner, 1991; Holekamp et al., 2012;) strictly defend their territories via severe aggression directed at potential immigrants by resident individuals. Finally, although in a more limited form compared to canids and hyenids, *L. catta* females (the dominant sex in this species) are able to form coalitions to preserve their dominance status or the possibility to use a territory (Soma & Koyama, 2013). These traits led us to predict that, as in other despotic but cooperative species (Jolly, 1966), reconciliation may be present in *L. catta* not only in captivity but also in the wild.

Prediction 2

In seasonal breeders, the mating period is a crucial time during which social behaviour changes dramatically (Clutton-Brock & Huchard, 2013). Majolo & Koyama (2006) found that in the population of despotic *Macaca fuscata* from Yakushima Island reconciliation was influenced by seasonality. As most lemur species, *Lemur catta* lives and has evolved in highly seasonal environment (Jolly, 1984; Wright, 1999) and females normally experience a single estrus per year, lasting a few hours (Evans & Goy, 1968; Koyama 1988; Cavigelli & Pereira, 2000) during which male-male competition is extremely high and females are particularly aggressive toward unwanted males attempting to mount (Jolly, 1966; Sussman & Richard, 1974; Sauther, 1991). Since ringtailed lemurs are seasonal breeders largely affected by seasonal variations, we predicted that reconciliation patterns could be affected by seasonality, more than by other factors.

METHODS

Ethics statement

Since the study was purely observational the Animal Care and Use board (University of Pisa) waives the need for a permit. The study was conducted with no manipulation of animals. The study was carried out in the private Reserve of Berenty (South Madagascar) and at the Pistoia Zoo (Pistoia, Italy). The owners, Mr De Heaulme (and family) and Mr Cavicchio permitted us to observe animals.

Study species

Lemur catta (ring-tailed lemur) is a diurnal species characterized by seasonal fluctuations in olfactory behavior, group dispersal, tolerance level, and reproduction (Jolly, 1966; Gould, 1999; Palagi, Telara & Borgognini Tarli, 2003; Palagi, Telara & Borgognini Tarli, 2004; Palagi & Norscia, 2009). *Lemur catta* shows a linear hierarchy, with females being dominant over males (e.g., Jolly, 1966; Kappeler, 1990; Souther, Sussman & Gould, 1999; Palagi, Telara & Borgognini Tarli, 2003; Koyama et al., 2005).

Even if the mating season overlaps among the different groups of a population (normally covering two months), the actual period of mating shifts from a group to another across about four months (Jolly, 1967; Sclafani et al., 2012). Females experience an annual estrus of a few days, with receptivity lasting 10–24 h (Jolly, 1966; Evans & Goy, 1968; Koyama, 1988; Cavigelli & Pereira, 2000; Souther, Sussman & Gould, 1999). If they do not get pregnant, a second or third belated estrus is possible (Jolly, 1966; Palagi, Telara & Borgognini Tarli, 2003; Palagi, Telara & Borgognini Tarli, 2004). *L. catta* females have a visible estrus, which is asynchronous with other females in their group (Pereira, 1991). They experience a genital swelling from about 1.5–3 cm in length and develop a pink center (Jolly, 1966). The mating period starts about one month before copulations, when the perineal area starts becoming increasingly larger and the center of genitalia increasingly larger and pinker: this period of swelling anticipates estrus (Jolly, 1966; Evans & Goy, 1968). Generally, receptivity coincides with the last day of maximal pink coloration of vaginal labia (Jolly, 1967; Evans & Goy, 1968).

Study location and subjects

Berenty (Madagascar)

We conducted the observation on wild lemurs in the gallery forest of Berenty, a reserve on the Mandrare River in Southern Madagascar (for an extensive description of the forest see Jolly et al., 2006). This research was conducted in the northern part of the forest called Ankoba (S

24.998; E 46.298), a 40-ha secondary forest 50- to 60-years-old, with canopy at 10–15 m (except for few emergent acacias to more than 20 m) and abundance of exotic plant species.

For this study we used the data collected in the periods November 2006-February 2007, April-July 2008, and March-April 2011 on five troops of *Lemur catta*. Details on group composition and observation periods are reported in Table 1. Kin relationships among group members were unknown. The individuals were well habituated to the presence of humans. Individual identification was based on sex and distinctive external features (Jolly, 1966).

Pistoia Zoo (Italy)

We studied three captive troops (here named A, B, and C) at the Pistoia Zoo (Italy) in the periods February-May 1999, November 2003-March 2004 and April 2004-February 2005. Details on group composition and observation periods are reported in Table 1. The lemurs were housed in an outside grassy enclosure (98 m2). 1999 groups A and B were kept in two separated indoor halls on the coldest days of the year (A: 10 m2 indoor facility; B: 20 m2 indoor facility). Large glass windows in the two indoor facilities allowed the lemurs to follow the natural day-light 24-h cycle. Each group utilized the outside enclosure for 4–6 h per day, separately. In 2003-2005, another group (C) was hosted at the zoo and could use the indoor facility previously used by group B. The observations started at the end of October 2003 and were stopped at the beginning of March 2004 to be resumed by other observers in late April 2004; meanwhile the group composition had changed with two infants becoming independent (thus turning into juveniles; Table 1) (for the ontogenetic development of *Lemur catta* see Gould, 1990; Palagi, Gregorace & Borgognini-Tarli, 2002). Therefore we analyzed the two periods separately, defining as group $C1_c$ (November 2003-March 2004) and group $C2_c$ (April 2004-February 2005). As in the wild, individual identification in captivity was based on sex and distinctive external features (Jolly, 1966).

Data collection

Systematic data collection was preceded by a training period that lasted until the observations by the observers (two) matched in 95% of cases (Martin & Bateson, 1986). The excellent visibility condition of the Berenty forest allowed us to apply in the wild the same protocol used in captivity. For each bidirectional agonistic encounter we recorded: (1) opponents; (2) aggressive behavioral patterns (mainly chase, bite, grab, jump); and (3) submissive/frightened patterns (flee and vocalization). The agonistic interaction was labeled as "decided" when one opponent gave up the fight (by retreating, fleeing or running away) and the winner could be therefore determined with certainty. For a comprehensive ethogram see Pereira & Kappeler, 1997.

After the last aggressive pattern of any given agonistic event, we followed the victim (as the focal individual) for a 10 min post-conflict period (PC). Matched control observations (MCs) took place during the next possible day at the same time and context (feeding, resting or travelling) as the original PC, on the same focal animal, in the absence of agonistic interactions during the 10 min before the beginning of the MC and when the opponents had the opportunity to interact, within a distance of 10 m (de Waal & Yoshihara, 1983; Kappeler & van Schaik, 1992).

We considered four groups of affinitive behaviors to identify the first conciliatory contact: body contact (body-to-body contact excluding tails, huddle); greeting (naso-nasal, face grooming); grooming (unidirectional, reciprocal or mutual); olfactory contact (sniffing body, sniffing genitals, and skin licking) (Pereira & Kappeler, 1997). We did not consider proximity as an affiliative behavior valid for reconciliation. We collected a total of 2339 PC-MC (1461 in captivity and 878 in the wild). For both PCs and MCs we recorded: (1) starting time; (2) type of first affinitive interaction; (3) minute of first affinitive contact; (4) partner identity.

Operational definitions and data analysis

Reconciliation analysis was carried out at the individual level. For each animal we determined the number of attracted, dispersed and neutral pairs over all PC-MC pairs. In attracted pairs, affinitive contacts occurred earlier in the PC than in the MC (or they did not occur at all in the

MC), whereas in dispersed pairs the affinitive contacts occurred earlier in the MC than in the PC (or they did not occur at all in the PC). In neutral pairs, affinitive contacts occurred during the same minute in the PC and the MC, or no contact occurred in either the PC or the MC (de Waal & Yoshihara, 1983). To evaluate individual reconciliation, we used the measure of corrected conciliatory tendency (CCT; Veenema, Das & Aureli, 1994), calculated as attracted minus dispersed pairs divided by the total number of PC-MC pairs. Individual CCTs were used to determine the mean CCT in wild and captive conditions. Due to the small sample size and/or deviation from normality (Kolmogorov-Smirnov, $p<0.05$) we used the Exact Wilcoxon signed-ranks test (Mundry & Fischer, 1998; Siegel & Castellan 1988) to compare attracted versus dispersed pairs at the individual level and therefore check for the presence of reconciliation.

We applied a General Linear Mixed Model (GLMM) to assess the effect of the different factors on individual CCTs (scalar, dependent variable). Data distribution was normal (Kolmogorov-Smirnov, p=n.s.) therefore an identity link function was used. As fixed factors, we considered sex (binomial: male/female), age (binomial: juvenile/adult) and rank position (ordinal), season (multinomial: 1-4), and setting (binomial: wild/captivity). Due to their inter-independence the factors sex, age and rank were entered as a combined variable (sex*age*rank). We tested models for each combination involving the variables of interest, spanning from the null model (only intercept) to the model including all the fixed factors (full model). To select the best model, we used the Akaike's Corrected Information Criterion (AICc), a measure for comparing mixed models based on the −2 (Restricted) log likelihood. The AICc corrects the Akaike's Information Criterion (AIC) for small sample sizes. As the sample size increases, the AICc converges to AIC. The model with a lower value of AIC was considered to be the best model. To avoid the increase of type II errors, factors were excluded from a model only if this improved the model fit by >2 AICc units. The value of degrees of freedom is given by the effective sample size (N) minus the rank design matrix of fixed effects (X). The denominator degree of freedom is estimated by SPSS via Satterthwaite's approximation.

We used all dyadic decided agonistic interactions to prepare a winner/loser socio-matrix and carry out hierarchical rank order analysis, by using MatMan 1.0 (Noldus Information Technology, Wageningen, Netherlands; de Vries, 1993). To assign the age class to each animal, the individuals were distinguished between adults (regularly performing genital marking, informing an age >18 months) and juveniles (not performing genital marking) (Palagi, Gregorace & Borgognini-Tarli, 2002).

Four seasons were recognized: lactation (1), pre-mating (2), mating (3), pregnancy (4) (The numbers correspond to how the seasons have been entered in the GLMM model). For the captive groups (in the northern hemisphere) the different seasons were: lactating season (group B_c: April-May 1999; group $C2_c$: April-August 2004); pre-mating (group $C2_c$: September-October 2004), mating (group $C1_c$: November-December 2003; group $C2_c$: November-December 2004), pregnancy (group A_c: February-March 1999; group $C1_c$: January-March 2004; group $C2_c$: January-February 2005) (Palagi, Telara & Borgognini Tarli, 2003). In the wild the mating period varied depending on the group (refer to Table 1 for the groups): pre-mating (group E_w: March-April: 2011), mating (group D_w: April-May-beginning of June 2008), pregnancy (group C_w: May-July 2008), and lactating season (groups A_w and B_w: November-February 2006) (Palagi, Telara & Borgognini Tarli, 2003). The mating period began when at least one female of the group started showing swelling (Sclafani et al 2012). Pregnancy started after the copulation days (confirmed ex-post by births) whereas lactation started when a female in the group gave birth.

RESULTS

A previous study (Palagi, Paoli & Borgognini-Tarli, 2005) showed that reconciliation was present in captive group A_c but not in group B_c (Table 1). The overall CCT was 10.25% ±2.24 (Mean

±SE). In the wild the CCT was 10.99% ±2.44 and in captivity 9.62% ±3.60 (Mean ±SE). For captive group C (Table 1) we found a significant difference between attracted and dispersed pairs in the period April 2004-February 2005 (exact Wilcoxon signed-ranks test, attracted>dispersed pairs; group C2$_c$: T=3, N=10, ties=1, p=0.020; Figure 1) but not in the period November 2013-March 2014 (group C1$_c$: T=8.50, N=10, ties=3, p=0.422). In the wild reconciliation was present in two groups out of five. We found a significant difference between attracted and dispersed pairs (attracted>dispersed) for group C$_w$ (T=0, N=12, ties=6, p=0.031; Figure 2a) and group E$_w$ (T=2.50, N=15, ties=6, p=0.020; Figure 2b). Instead, no significant difference between attracted and dispersed pairs was found for group A$_w$ (T=0, N=8, ties=4, p=0.125), group B$_w$ (T=12, N=11, ties=2, p=0.254) and group D$_w$ (T=19.50, N=18, ties=7, p=0.254).

Of all the GLMM models tested (AICc range= 726.852-1014.252) the best one was the full model (F=1.123, df1=35, df2=75, p=0.331), including the combination of individual features (sex*age*rank; F=0.805, df1=31, df2=75, p=0.746), the setting (wild/captivity; F=1.609, df1=1, df2=75, p=0.209), and the season (lactation, pre-mating, mating, and pregnancy; F=3.358, df1=3, df2=75, p=0.023). Only the season had a significant effect on the distribution of CCTs across individuals. Figure 3 shows the CCT fluctuations across seasons.

DISCUSSION

Reconciliation was present both in the wild and in captivity (prediction 1 supported), and specifically in two out of five wild troops of *Lemur catta* (Figure 2) and in two captive troops (group C2$_c$: present study; group A$_c$: Palagi, Paoli & Borgognini-Tarli, 2005) (Figure 1). Season, more than any other factor tested in the analysis, best explained the fluctuation in the frequency of reconciliation events (prediction 2 supported). In fact, the conciliatory tendency was lowest during the mating season and highest during pregnancy (Figure 3).

Reconciliation was found in another despotic species, the wolf (*Canis lupus*; mean conciliatory tendency, 44.1% in the wild: Baan et al., 2014; 53.3% in captivity: Cordoni & Palagi, 2008). Within a pack, every wolf knows its social standing with every other individual and each group defends its own territory as a unit (as *Lemur catta* troops do). Yet, even if the alpha male normally guides the movements of the wolf pack and initiates aggressions against intruders (Mech, 1977), the subordinate members can sometimes oppose their leader's actions. According to Zimen (1981), no subject decides alone the carrying out of activities that are vital to the group cohesion. In short, wolves are highly despotic but also extremely cooperative. The existence of an extremely cooperative pack has presumably to do not only with hunting but also with the collective rearing of offspring and, consequently, with reproductive success (Mech & Boitani, 2003). It is clear that in wolves the benefit of reconciling and preserving the social bonds outweighs the cost deriving from pack disruption, which would be detrimental for both dominants and subordinates. Thus, reconciliation can be found in despotic groups provided that they show some form of cooperation. Further evidence of this assumption is the presence of reconciliation in spotted hyenas (*Crocuta crocuta*; Wahaj et al., 2001). Hyenas are despotic but often depend on the help from other group members during hunts, defence of ungulate carcasses against competitors, and coalition formation that is important in both the acquisition and maintenance of social rank (Wahaj et al., 2001). Cooperation and despotism are two opposite forces that contribute in shaping reconciliation patterns, as it becomes especially clear when comparing species differing only in some aspects of the social system. In hyenas, as in wolves, the necessity to cooperate overcomes the competition between dominants and subordinates, which explains the presence of reconciliation. The lower levels of reconciliation observed in hyenas (mean conciliatory tendency: 11.3%; Wahaj et al., 2001) may be due to the fact that, contrary to wolves, spotted hyenas live in a fission fusion society allowing dispersal (other than reconciliation) as an exit strategy. The influence of the cooperation pressure over the suitability of engaging in reconciliation is even more evident when comparing spotted hyenas with ringtailed lemurs. Although both species possess steep female dominance, they strongly differ in the level of cooperation. Different from hyenas, cooperation in *Lemur catta* is limited to the coalitionary support provided to the dominant female by other females during target aggression toward conspecifics (usually to evict them from the group or the core area of the home range; Vick & Pereira, 1989). This limited cooperation can explain why the mean conciliatory tendency in *Lemur catta* (9-10%) is lower than in hyenas and wolves.

Although at low levels, reconciliation is possible when the cooperation-competition balance tilts in favor of cooperation because the benefits of peace making overcome the costs of leaving conflicts unmanaged. But when reproduction is at stake, as it is in lemurs during the once-a-year mating period, competition is so high (Jolly, 1966; Starling et al., 2010) to prevent conflicts to be peacefully resolved. In this period the goal is reproduction more than social stability.

In this study we found that reconciliation is season-dependent in *Lemur catta* (Figure 3). This result is confirmed by the only study that to date has investigated the seasonal fluctuations of reconciliation in another despotic primate species (Majolo & Koyama, 2006). In their article, Majolo & Koyama (2006) reported that in female Japanese macaques (*Macaca fuscata*) mating - and not other factors such as changes in activity budgets and dietary composition - had profound effects on peace-making. In fact, the conciliatory tendency was significantly lower during the mating season than in the non mating season (Majolo & Koyama, 2006). The authors commented that the negative effects of the mating season on reconciliation within female Japanese macaques may be due to the relevance of female competition for the access to male partners in multimale, multifemale societies characterized by adult male dominance. In *Lemur catta* the situation is reversed: adult females are dominant over males (Jolly, 1966; Sauther, Sussman & Gould, 1999; Sclafani et al., 2012), and the competition and stress levels during the mating period are highest among males for the access to female partners (Starling et al., 2010). Despite the twist in the dominant sex between *Lemur catta* and *Macaca fuscata*, the result is similar: reconciliation is lowest during the extremely high competitive mating period.

A proxy of the seasonal distribution of reconciliation can lie in how hormones modulate the propensity to affiliate with others, and consequently to reconcile. It is worth reminding that the very definition of reconciliation implies the use of affinitive contacts for peace making (de Waal & van Roosmaleen, 1979). During the mating period stress hormones are highest in *Lemur catta* males (Starling et al., 2010). Stress hormones can elicit the fight or flight response (Sapolsky, 1990) leaving little space for post-conflict affiliation to males. Moreover, as well as in other animals in which the sexual context is associated with aggression and competition (Goldey & van Anders, 2014; Barrett et al., 2002), *Lemur catta* males experience highest levels of testosterone during the extremely high competitive mating period (Gould & Ziegler, 2007), which also coincides with the lowest levels of inter-male affiliation (Gabriel, Gould & Kelley, 2014). Additionally, the highest levels of estradiol associated with the mating period can reduce affiliation between primate females, as it occurs in rhesus monkeys (*Macaca mulatta*; Wallen & Tannenbaum, 1997). The hormonal influence may partly explain why post-conflict affiliation is virtually absent in *Lemur catta* during mating (Figure 3). Similarly, the influence of other hormones – namely oxytocin (Campbell, 2008) - may explain why post-conflict affiliation is highest during pregnancy in *Lemur catta* (Figure 3), especially considering that the conciliatory contacts in *Lemur catta* are mainly initiated by adult females (Palagi, Paoli & Borgognini-Tarli, 2005). Oxytocin, reaching its climax during pregnancy, enhances the individual propensity to affiliate in humans (Feldman, 2012) and other primate and non-primate mammals (Drago et al., 1986; Smith et al., 2010a), being especially relevant for maternal care and social attachment (Turner et al., 1999; Zak, 2005; Campbell, 2008). Also prolactin - highest during lactation - enhances parental behaviour and seems to favour social propensity (Botchin et al., 1993; Gettler et al., 2012). High levels in the “affiliation hormones” may account for the increased levels of conciliatory tendency of *Lemur catta* in the post-mating period, also after pregnancy (Figure 3). The seasonal fluctuations of conciliatory affiliation in *Lemur catta* documented in the present study are also consistent with the variation of inter-male affiliation rates recorded by Gabriel, Gould & Kelley (2014) in the same species, in four sites of Madagascar. These authors observed that inter-male affiliation levels varied across reproductive periods, with the highest frequencies being observed during the gestation and lactation/migration periods and the lowest frequencies occurring during the mating period. Gabriel, Gould & Kelley (2014) postulated that inter-male affiliative relationships in *Lemur catta* may provide beneficial social interactions when females are unavailable. Overall, the seasonal fluctuations of the reconciliation tendency observed in *Lemur catta* appear to be sustained by both physiological and socio-ecological data.

Reproduction is not the only resource worth competing for. Food also represents a valuable stake for the members of social groups, eliciting competition more than cooperation. This is particularly true in lemurs which do not rely on cooperation to seek food because they are normally characterized by a folivorous-frugivourous diet (Ganzhorn et al., 2009). Consistently, in the wild reconciliation was found in a group of *Eulemur rufus x collaris* and in two groups of *Propithecus verreauxi* but never in the feeding context (Palagi et al., 2008; Norscia & Palagi, 2011). This situation reinforces the idea that when a valuable resource is concerned and cooperation is low (e.g. mate for reproduction, high energy food), gaining the access to that resource can be more rewarding than repairing the relationship with a former opponent in the short term, via post-conflict reunions.

CONCLUSIONS

The model species used in this study belongs, as humans, to the primate order, which is characterized by a stunning variety of social structures (Fleagle, 2013; Kappeler & van Schaik, 2002). Humans have “experimented” most of them, with the two poles of the tolerance axis being represented by hierarchical and cooperative structures, since Neolithic (Meter, 2014). As in non-human primates (Kappeler 1993; Thierry 2000), the levels of cooperation versus authority exerted by conspecifics influence the way conflicts are managed in human societies (coercion versus friendly reunion), in which cooperation is associated with peaceful conflict management (e.g. in nomadic foragers; Fry, 2012). The present investigation supports the hypothesis that the ability of reconcile has been favored by natural selection evolution also in highly despotic species to be used when it is convenient. Consistently, such ability is expressed when the benefits of intra-group cooperation are not annihilated by competition, as it occurs when a limited, valuable resource is at stake. In summary, this study shows that in despotic social groups in which coalitions are observed, the right question is not *if* but *when* reconciliation can be present.

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Figures

Figure 1 – Box plot showing the significant difference (Exact Wilcoxon's test, $p<0.05$) between the number of attracted versus dispersed pairs in the *Lemur catta* troop C2c (April 2004-February S2005), observed at the Pistoia Zoo (Italy). Solid horizontal lines indicate medians; the length of the boxes corresponds to inter-quartile range; thin horizontal lines indicate range of observed values.

Figure 2 – Box plot showing the significant difference (Exact Wilcoxon's test, $p<0.05$) between the number of attracted versus dispersed pairs in two wild *Lemur catta* troops (C_w: May-July 2008, figure 2a on the left; E_w: March-April 2011, figure 2b on the right) observed in the Berenty Forest (Madagascar). Solid horizontal lines indicate medians; the length of the boxes corresponds to inter-quartile range; thin horizontal lines indicate range of observed values.

Figure 3 – Error bars showing mean±SE of individual corrected conciliatory tendency (CCT, %) in the different seasons of the year. Season is the only factor that significantly influence the CCT distribution in the study groups (GLMM; $F=3.358$, $df1=3$, $df2=75$, $p=0.023$). The conciliatory tendency % is lowest during mating and highest during pregnancy.

Figure 1

Attracted pairs are significanly more than dispersed pairs in a captive *Lemur catta* troop

Box plot showing the significant difference (Exact Wilcoxon's test, $p<0.05$) between the number of attracted versus dispersed pairs in the *Lemur catta* troop C2c (April 2004-February S2005), observed at the Pistoia Zoo (Italy). Solid horizontal lines indicate medians; the length of the boxes corresponds to inter-quartile range; thin horizontal lines indicate range of observed values.

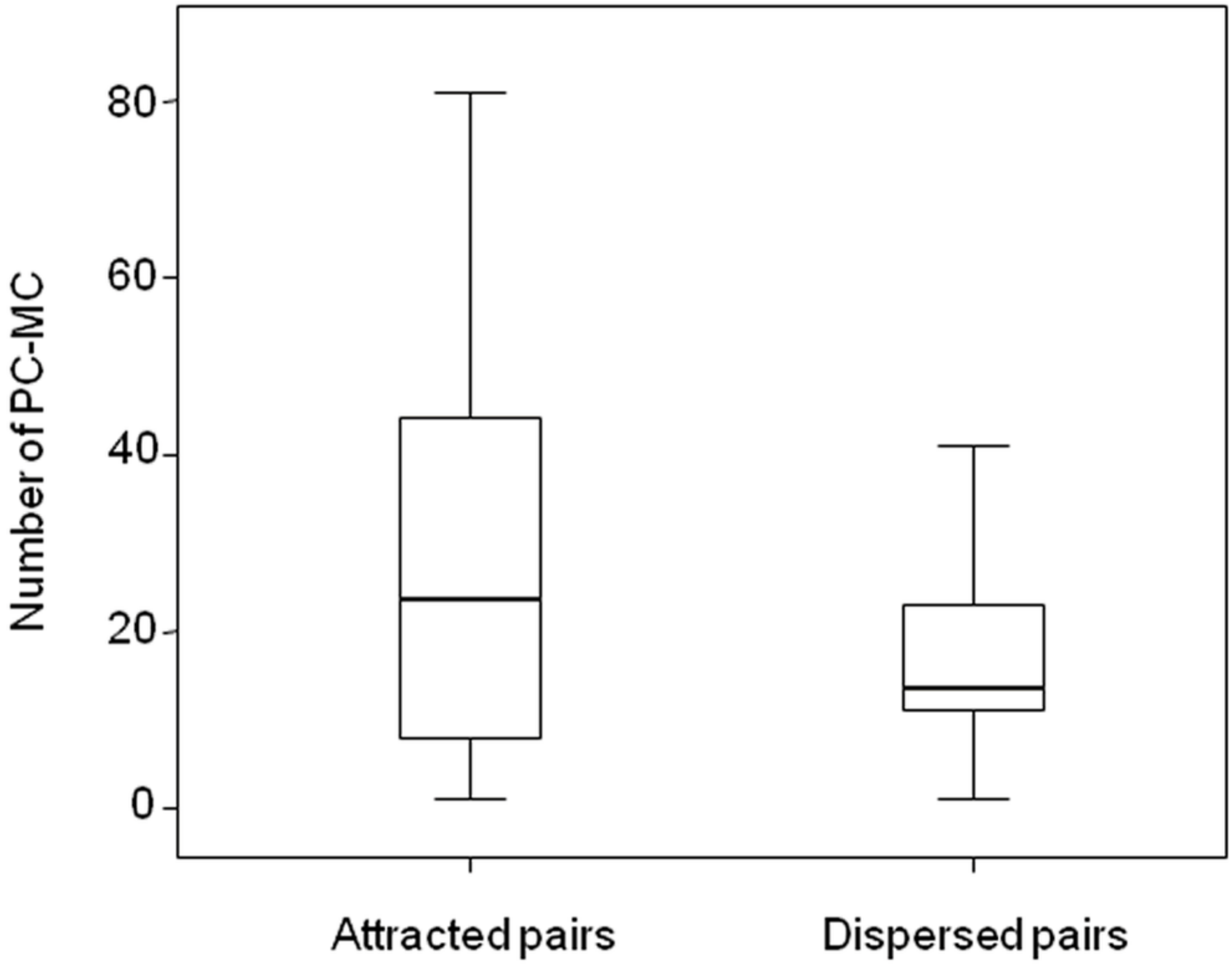

Figure 2

Attracted pairs are significantly more than dispersed pairs in two wild troops of Lemur catta

Box plot showing the significant difference (Exact Wilcoxon’s test, $p<0.05$) between the number of attracted versus dispersed pairs in two wild *Lemur catta* troops (Cw: May-July 2008, figure 2a on the left; Ew: March-April 2011, figure 2b on the right) observed in the Berenty Forest (Madagascar). Solid horizontal lines indicate medians; the length of the boxes corresponds to inter-quartile range; thin horizontal lines indicate range of observed values.

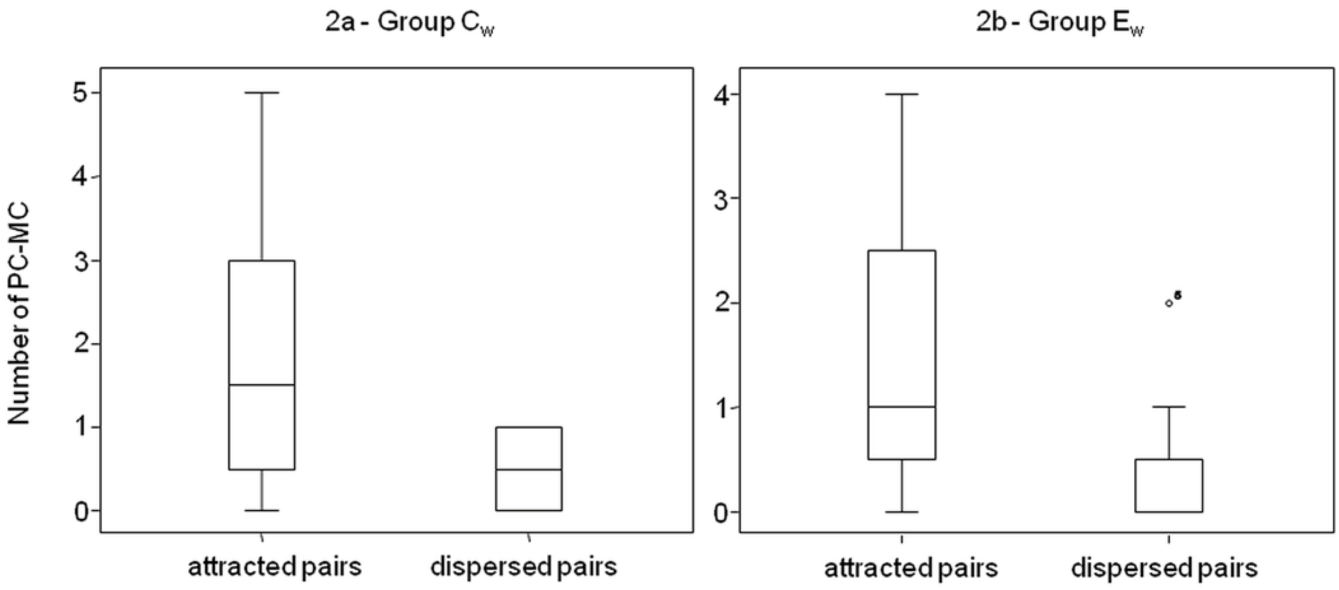

Figure 3

Seasonal fluctuations of conciliatory tendencies in *Lemur catta* troops. The propensity to reconcile is lowest during mating and highest during the pregnancy period.

Error bars showing mean±SE of individual corrected conciliatory tendency (CCT, %) in the different seasons of the year in *Lemur catta*. Season is the only factor that significantly influence the CCT distribution in the study groups (GLMM; F=3.358, df1=3, df2=75, p=0.023). The conciliatory tendency % is lowest during mating and highest during pregnancy.

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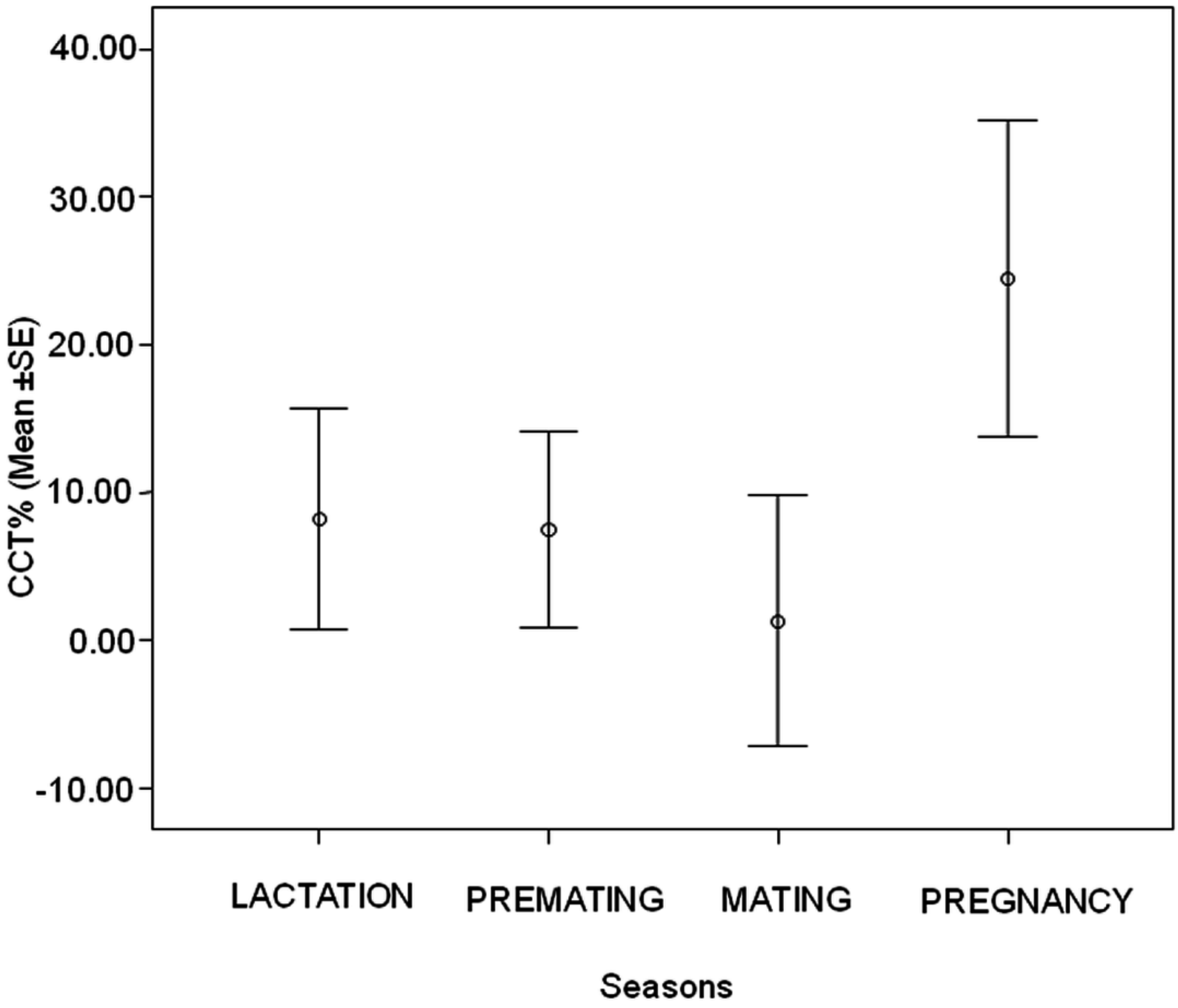

40.00
30.00
20.00
10.00
0.00
-10.00
CCT% (Mean ±SE)
LACTATION
PREMATING
MATING
PREGNANCY
Seasons

Table 1(on next page)

Study groups, periods and location

Composition of wild and captive groups, observation periods and study sites.

Table 1 - Composition of wild and captive groups, observation periods and study sites.

Group	**Period**	**Males**$_{\textbf{adult}}$	**Females**$_{\textbf{adult}}$	**Males**$_{\textbf{juvenile}}$	**Females**$_{\textbf{juvenile}}$	**Study site**
						WILD
A_w	Nov$_{2006}$-Feb$_{2007}$	4	4	1	0	Berenty
B_w	Nov$_{2006}$-Feb$_{2007}$	4	6	2	1	Berenty
C_w	May-Jul$_{2008}$	3	6	1	2	Berenty
D_w	Apr-Jun$_{2008}$	6	8	1	3	Berenty
E_w	Mar-Apr$_{2011}$	5	5	5	2	Berenty
						CAPTIVITY
A_c	Feb-Mar$_{1999}$	2	3	0	0	Pistoia
B_c	Apr-May$_{1999}$	2	4	2	0	Pistoia
$C1_c$	Nov$_{2003}$-Mar$_{2004}$	4	4	0	0	Pistoia
$C2_c$	Apr$_{2004}$-Feb$_{2005}$	4	4	0	2	Pistoia

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