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1	A resident-nepotistic-tolerant dominance style in wild white-nosed coatis (Nasua narica)?
2	Short title: Dominance style in white-nosed coatis
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Summary

Dominance relationships imply consistent asymmetries in social relationships. Socioecological models predict that resource distribution determines the mode of competition that animals will face and, ultimately, the nature of their social relationships. Here, we provide the first systematic investigation of dominance style in white-nosed coatis (Nasua narica). Coatis live in cohesive female-resident groups, and have a diet based on clumped (fruits) and dispersed (insects) food items, which are predicted to favour despotic and egalitarian social styles, respectively. Our results revealed moderate linearity and steepness in dominance relationships over time, with variations attributed to stages of reproductive season, rather than presumed variations in food resources. Primary social bonds and coalitions were found to mediate dominance rank. Overall, our results suggest some similarities between coatis and despotic-tolerant primate species, at least under particular ecological circumstances, and we discuss their potential for affording a deeper understanding on the sources of variation in mammal social systems.

Keywords

Dominance, Agonistic conflicts, Social structure, Socioecological model, Mammal societies

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Introduction

Dominance relationships are a key component of animal societies (Pusey & Packer, 1997; Sterck et al., 1997; Smith et al., 2007; Pellegrini, 2008; Shizuka & McDonald, 2012, 2015; Lea et al., 2014; Hobson & DeDeo, 2015). Dominance exists when one individual consistently prevails over another individual during social conflict, resulting in a dominant-subordinate relationship which describes the direction of power balance within a dyad (Hand, 1986; Drews, 1993; Preuschoft & van Schaik, 2000). Where the outcomes of social conflicts are consistent within and between dyads in a social group, individuals can be ranked in an order of dominance (i.e. a hierarchy of dominance). From a functional point of view, establishing dominance relationships allows individuals to avoid both the cost of a continuous assessment of others' fighting abilities and the risk of escalation (Clutton-Brock & Harvey, 1976; Hand, 1986). This process is expected when (i) individuals meet repeatedly (Drews, 1993; Preuschoft & van Schaik, 2000), (ii) there is competition for resources (Clutton-Brock, 2009; Lea et al., 2014) and (iii) rank confers some priority of access to them (Kappeler, 1993; Clutton-Brock, 2009; Clutton-Brock & Huchard, 2013a; but see Hand, 1986; and Drews, 1993, for an alternative view). Long-term benefits for dominant individuals are likely and correlations between dominance status and fitness-relevant measures are well documented (see Sapolsky, 2005; Clutton-Brock & Huchard, 2013a,b; Lea et al., 2014; Habig & Archie, 2015).

In general, dominance hierarchies are characterized by two main properties: linearity and steepness (de Vries et al., 2006). A hierarchy is perfectly linear when all dominance relationships are transitive (i.e. A > B, B > C, C < A). The more linear the hierarchy, the more rigidly organized and predictable the dominance relationships are (Isbell & Young, 2002). Steepness represents the magnitude of differences in winning success among individuals (de Vries et al., 2006). When a hierarchy is shallow these differences are small, whilst the steeper the hierarchy the larger the asymmetries in winning success are (i.e. the dominance relationships are more despotic: Vervaecke et al., 2007). Both properties are complementary and enable researchers to characterize and compare dominance structures of animal groups.

Whilst causes of variation in dominance structure of groups remain elusive (Clutton-Brock, 2009), socioecological models (Wrangham, 1980; van Schaik, 1989; Sterck et al., 1997) predict that once group living has evolved, the distribution of food resources determines the mode of competition that animals will

face (i.e. contest vs. scramble competition, within- vs. between-group competition), which in turn determines the nature of their social relationships (reviews in Isbell & Young, 2002; Ostner & Schülke, 2012). These socioecological models represent the most comprehensive attempt to explain the causes of variation in social structure of groups, but are not exempt of criticism (e.g. Janson, 2000; Thierry, 2008; Koening & Borries, 2009) and are seldom applied to non-primate animals, including those which are similar to primates in terms of their ecology and social organization (see Clutton-Brock, 2009).

Coatis (*Nasua spp.*) are the most gregarious species within the family Procyonidae (Mammalia: Carnivora), forming groups ('bands') that vary in size from five up to 31 individuals (see Hirsch & Gompper, 2017). Coati bands (*Nasua spp.*) are usually constituted by closely related adult females (i.e. the philopatric sex) and their offspring, whilst males are pronouncedly less gregarious (Gompper, 1995; Gompper & Decker, 1998; but see Hirsch, 2011). Gompper (1996) claimed that intersexual foraging competition over clumped food sources may have promoted female gregariousness, thus allowing females to drive off and even to defeat the larger and stronger coati males which otherwise tend to prevail in one-to-one encounters. Although various studies have addressed different aspects and consequences of coatis' social behaviour (e.g. Kaufmann, 1962; Smythe, 1970; Smith, 1977; Russell, 1983; Gompper & Krinsley, 1992; Gompper, 1996; Gompper et al., 1997; Booth-Binczik, 2001; Haas & Valenzuela, 2002; Romero & Aureli, 2007, 2008; Hirsch & Maldonado, 2011; Hirsch et al., 2012), including careful descriptions of their agonistic interactions, only one study (Hirsch, 2007) has provided a systematic evaluation of their dominance relationships.

Coatis tend to forage primarily on invertebrates and fruits, which together account for more than 85% of their diet (Gompper & Decker, 1998; Valenzuela, 1998; Balaguera-Reina et al., 2009; Hirsch, 2009; Booth-Binczik, 2001), although the relative importance of invertebrates versus fruits varies across species, populations, and seasons (see Valenzuela, 1998; Rodríguez-Bolaños et al., 2000; Alves-Costa et al., 2004). A reliance on invertebrate prey – which tends to occur unpredictably in small, rapidly consumable quantities (Gompper, 1996; but see Redford, 1984) – is expected to favour scramble competition and more egalitarian social relationships (Isbell, 1991; Sterck & Steenbeek, 1997; Sterck et al., 1997; Isbell & Young, 2002). Accordingly, it was assumed for years (without further evidence) that coatis do not form dominance hierarchies (Kaufmann, 1962; Smith, 1977; Gompper, 1995; Gompper et al., 1997). In contrast, a primarily

frugivorous diet – where high quality resources tend to be distributed in predictable and defendable patches – should favour strong intra-group contest competition which, in turn, promotes the formation of more despotic/hierarchical social structures (van Schaik, 1989; Isbell, 1991; Vogel et al., 2007; Johnson et al., 2009; Wright & Robbins, 2014). Indeed, among white-nosed coatis (*N. narica*) in Barro Colorado, Panama, the majority of aggressive conflicts occur over fruits (55% of observations: Gompper, 1996; but see Booth-Binczik, 2001) and ring-tailed coatis (*N. nasua*) living in Iguazú National Park, Argentina, compete for Pindo palm fruits (*Syagrus romanzoffianum*) which are directly responsible for as much as 33.6% of all agonistic conflicts, and result in a sex/age class based dominance structure (Hirsch, 2007). In fact, in Iguazú National Park juvenile coatis are dominant over most of the group members (except adult males), largely because of the regular agonistic support they receive from adult females (Hirsch 2007). Regular third-party support during agonistic conflicts was also reported by Kaufmann (1962) and Gompper et al. (1997) among the white-nosed coatis of Barro Colorado, although no evidence for dominance relationships was found there (but sociometrics were not reported). Therefore, despite coalitions representing a common event during coati conflicts (see also Romero & Aureli 2008), it remains unknown whether they lead to the establishment of a dominance hierarchy.

We investigated whether and how a band of n=23 wild white-nosed coatis living in the surroundings of 'El Tepozteco' archaeological site (Tepoztlán, México) maintain dominance relationships, and explored their basic properties in terms of linearity, steepness, and stability over eight months of observation. Given observations of philopatric females directing aggressive behaviour towards subadults (Gompper et al., 1997; Hirsch, 2007) and adult males (Kaufman, 1962; Gompper, 1995; but see Booth-Binczik, 2001; Hirsch et al., 2012) and reports of common coalitionary support during agonistic conflicts (*N. narica*: Gompper et al., 1997; *N. nasua*: Hirsch, 2007; Romero & Aureli, 2008) we expected sex, age, and social support to structure dominance interactions and hierarchy, whereby females will rank above males, juveniles and adults over subadults, and those animals from the largest subunits (see Methods) and participating more in coalitions will outrank those with fewer potential allies or less involved in coalitions. In addition, because coati diet is largely based on a combination of defendable (i.e. fruit) and indefensible (i.e. invertebrates) resources, we expect coati dominance to lie midway between despotic and egalitarian social styles; i.e. we predict a linear dominance hierarchy but shallow dominance gradient. However, based on the reported characteristics of coati

diet in tropical dry forests (see Valenzuela, 1998; Valenzuela & Macdonald, 2002), where food resources show seasonal patterns in their spatio-temporal distribution and defensibility (see below), we also expected to see changes in the steepness and linearity of dominance hierarchy as a consequence of the presumed variation in levels of competition over food resources. We expected more despotic dominance relationships (i.e. steep and linear dominance hierarchies) during the driest months of the study (February to late May), when seasonal and potentially defendable food sources become available (i.e. fructifying trees: Valenzuela, 1998; Valenzuela & Macdonald, 2002). In contrast, we expected more egalitarian dominance relationships during the rainy season (June to September), as high quality but usually non-defendable resources become abundant (i.e. invertebrates: Valenzuela, 1998; Valenzuela & Macdonald, 2002; Márquez, 2003; Toledo-Hernández et al., 2015). A similar pattern was also expected regarding the general characteristics of coati conflicts, with more intolerant agonistic interactions (i.e. less frequent but more intense aggression and less instances of counteraggression) during the dry season, and more tolerant ones during the rainy season.

Material and methods

Study subjects and site

The study was conducted from January to October 2014 on a community (sensu Wells et al., 1987) of free-ranging white-nosed coatis of both sexes and all age classes, inhabiting the surroundings of the archaeological site El Tepozteco (19° 0' 2"N, 99° 6' 4"W) in Tepoztlán, México (Central Mexico). We selected a band of n=23 animals (2 adult males, 7 adult females, 4 subadult females, 2 juvenile males, and 8 juvenile females) for behavioural sampling and statistical analyses, on the basis of their regular presence at the archaeological site and our ability to identify individuals accurately (see Table S1 in Supporting Information). Age classes were defined after Gompper (1996) and Hirsch (2007) as follows: juveniles (< 1 year old.), subadults (between 1 and 2 years old), and adults (> 3 years old). All juveniles were at least six months old at the start of the study. Behavioural data from four additional individuals were also collected, but we did not include them in our present analyses because those individuals (plus two unidentified ones) appeared to belong to another band.

The archaeological site is located on the top of the Tepozteco mountain (2310 m.a.s.l.), within the protected El Tepozteco National Park - Chichinautzin Biological Corridor (Trans-Mexican Volcanic Belt).

The surroundings of the site present an irregular surface with steep slopes, raised cliffs, and deep ravines. Temperate sub humid climate (i.e. rainy and hot summer, dry winter) and an ecotone of tropical dry forest characterize the study area (CONANP, 2008). June to September period accounted for 75% of the 2014 annual precipitation (1393 mm) (http://clima.inifap.gob.mx/redinifap/est.aspx?est=35883).

The tropical dry forest habitat provides fleshy fruits and litter arthropods consumed by coatis (Valenzuela, 1998; Valenzuela & Macdonald, 2002), and several species of fig trees (Ficus sp.) can be found at the study site (pers. obs.), which fruit once or twice between September-February (Piedra-Malagón et al., 2006) and serve as food sources for the coatis. Other potential sources of fruit include wild grapes (Vitis tiliifolia), red mombin (Spondias purpurea), red nanche (Malphigia mexicana) (pers. obs.), as well as species from Ericaceae, Garryaceae, Verbenaceae, Onagraceae, Fabaceae, and Myrtaceae families (remains of fruits of those families have been found in the faeces of coatis at the study site; F. Gómez-Sánchez, pers. comm.). Litter arthropods have been reported by Valenzuela (1998) as part of the coatis' diet in a tropical dry forest and include scorpions (Arachnida: Scorpiones), grasshoppers and crickets (Insecta: Orthoptera), and whitegrubs/beetles (Phyllophaga spp.). Orthopterans and beetles become abundant during the rainy season (pers. obs.) and, along with myriapods (Arthropoda: Myriapoda), represent the most common invertebrates in coati faeces at the study site (F. Gómez-Sánchez, pers. comm.). Since El Tepozteco is a highly visited tourist attraction, coatis also have access to anthropogenic food sources. Although visitors are prohibited from both feeding animals and entering the archaeological site carrying food, the coatis do consume human-derived food items. In fact, remains of this food appeared in 20% of all examined coati faeces (F. Gómez-Sánchez, pers. comm.), and one of each six agonistic conflicts (17.41%) occurred over anthropogenic food sources (Table 1).

Behavioural observations

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Coatis at the site are habituated to humans and we were able to follow them closely (~ 2 m), without any apparent disturbance, and all individuals were individually identifiable by ear tags and/or physical features. Ear tags (Nasco Rototags, Fort Atkinson, Wisconsin, USA) were fitted during routine captures (License of Scientific Collection FAUT-0251 granted by SEMARNAT to DV-G) conducted according to the ASAB's "Guidelines for the treatment of animals in behavioural research and teaching", and the Mexican law NOM-126-SEMARNAT-2000.

Behavioural data were collected from February to the first week of October 2014 from Monday to Friday (tourist numbers were higher during weekends and interfered with observations). We conducted observations of the coatis over four broad periods that corresponded to the following events: mating season/early dry season (February-March), gestation period/late dry season (April-May), birth and nesting period/early rainy season (June-July), and young's early socialization/late rainy season (August-early October). Behaviours were identified on basis of the ethograms of Kaufmann (1962) and Smith (1977) and observations began as soon as animals arrived at the archaeological site from ravines/mountainsides and continued until the archaeological site's closing (1730 h). Hourly instantaneous scan samples (Altmann, 1974) were conducted by walking through the site and scoring each animal's behaviour when first detected. Animals that were not observed during 20 minutes were considered absent for that scan. We carried out 15-min continuous focal observations (Altmann, 1974), once per day/individual at randomly allocated time slots, resulting in a mean±SD of 43.87±7.88 focal observations per animal (Table S1). Complementarily, we opportunistically recorded every agonistic and grooming interaction (ad libitum sampling: Altman, 1974).

After mating season, pregnant females reduced the time they spent with the band, but were only completely isolated from the band for ~ one week after giving birth. We were therefore able to collect behavioural data on females during pregnancy and post conception. The two adult males in this study were associated with the band throughout the study period, which is not typical (Kaufmann, 1962; Gompper, 1995), and we were able to conduct a similar number of focal samples on each sex (Table S1).

Agonistic interactions (conflicts)

During agonistic interactions, animals which showed submissive behaviour towards their opponent were classified as the 'loser' and the opponent became the 'winner'. Submissive behaviour was recognized when an animal retreated or fled in response to the approach or aggression from another individual (see Table S2 for detailed behavioural definitions). Displacements, where an individual retreated from an approaching individual were also recorded as submissive behaviours, with the former was considered the loser (and the approaching individual considered the winner). Otherwise, the outcome of the agonistic interaction was classified as undecided. Interactions were defined as unidirectional (i.e. just one animal attacked) or involving counter-aggression (i.e. the victim reacted by attacking its former aggressor). After Butovskaya (1993), we

discriminated aggressive behaviour in two categories depending on whether physical contact took place; i.e. contact vs. non-contact aggression. Where interactions involved two or more animals acting together against a third-party (i.e. 'coalitions', see Table S2), we recorded the identities of each animal involved, and recorded detailed winner-loser interactions at a dyadic scale. An interaction was considered to have finished when opponents stopped and did not restart performing aggressive behaviours during the next 30 seconds.

We computed the rate of conflicts per hour, the trigger of the conflicts when evident, the percentage of these which involved counter-aggression, coalitions, or remained undecided, as well as the percentage of contact aggressions. Rates per hour were computed exclusively from focal sampling data. We assessed these parameters in order to better characterize the dominance style of coati society. For example, in the well-studied genus *Macaca* (Primates: Cercopithecidae), occasional but severe aggression and scarce counteraggression during conflicts are expected in the more intolerant species (e.g. *M. mulatta, M. fuscata;* see Thierry, 2000; Balasubramaniam et al., 2012), whilst the opposite is expected for the more tolerant ones (e.g. *M. tonkeana, M. sylvanus*; see Thierry, 2000; Duboscq et al., 2013).

Grooming interactions and adult-young units

A grooming bout was defined as individuals grooming without interruptions of more than 10 seconds. Otherwise, it was scored as a new grooming bout (see Table S2). After a few days observing coatis' interactions, it became evident that young individuals tended to segregate into subunits by associating with a given adult female. We used rates of grooming to determine the composition of such associations. Only data on unidirectional (i.e. non-mutual) grooming bouts (n= 723), collected during focal and ad libitum samples, were used. For all individuals, we computed the cumulative binomial probability for at least (i.e. the same or more) the amount of grooming received from each band member, relative to the overall individual grooming received

$P(X \ge x)$

where X denotes the event we are interested in (i.e. the grooming received from a given individual), and x denotes the observed frequency of grooming received from that individual. Then, we considered as carer-young dyads those composed by an adult female and a juvenile/subadult, whose cumulative probability

was ≤ 0.001. Those juveniles/subadults sharing a grooming bond with the same adult female were considered members of the same subunit, as they largely represent adult females' local grooming network. Together, the adult female and the non-adult individuals attached to her constituted what we called an 'adult-young unit'. We preferred this more cautious term rather than 'matrifocal unit' (sensu Fedigan, 1992), because coati species have been reported to perform allonursing (McToldridge, 1969; Russell, 1983), thus raising the possibility that young end up attached to an adult female different to their mother. Therefore, we cannot assure that all the dyads within adult-young units represent mother-offspring or sibling relationships.

Dominance hierarchy

In order to test whether expected changes in food availability altered patterns of dominance and aggression, and to control for any effects of mating seasons, we assessed the coati dominance hierarchy over the foregoing observational periods (see above). Then, we constructed four squared sociometric matrices (Tables S3, S4, S5 and S6) for the corresponding periods from all decided agonistic conflicts (i.e. those where a winner and loser could be identified, see Hausfater, 1975), including polyadic ones. From each matrix we computed the number of undecided relationships (i.e. tied and unknown), the Normalized David's Scores (NDS) (de Vries et al., 2006), the improved Landau's linearity index (de Vries, 1995), and the steepness (i.e. the slope of the regression line when plotting the ordinal dominance rank vs. its corresponding NDS) of the resulting dominance hierarchy (de Vries et al., 2006). We also assessed these parameters for the whole dry and rainy seasons. These analyses were conducted using the compiled version of SOCPROG 2.6 (Whitehead, 2009), and the Steepness 0.2-2 (Leiva & de Vries, 2014) and Compete 0.1 (Curley, 2016) packages for R environment (R Development Core Team, 2013). By convention, animals hold an ordinal rank inverse to their NDS; i.e. the first ordinal number belongs to the animal with the highest NDS and the last ordinal number represents the animal with the lowest NDS.

To further evaluate the power asymmetries, we computed three group-level measures on the equality/unbalance in aggression direction. First, an average reciprocity index for aggression was computed for each of the four periods (Silk et al., 1999). The index ranges from zero to one, where values near to zero indicate that aggression was mostly unidirectional across the dyads (i.e. not reciprocated) and values close to

one indicate that aggression was evenly performed (or that no aggression occurred at all). The index is computed as follows:

$$RI = \frac{\sum_{i}^{n} \frac{P_{ab}(X \le x)}{P_{ba}(X \le x)}}{k}$$

where n represents all instances of aggressive behaviour observed for the ij dyad, $P_{ab}(X \le x)$ represented the cumulative binomial probability of aggression in the least frequent direction observed within a dyad, $P_{ba}(X \le x)$ represented the cumulative binomial probability of aggression in the most frequent direction observed within a dyad, and k represented the total number of dyads observed. Second, we computed the average directional consistency index for aggression (DCI) across the four periods (van Hoof & Wensing, 1987). The DCI represents a measure of the skew in the direction of a behaviour across dyads. The DCI ranges from zero to one, where values near to zero indicate that the behaviour is evenly performed between the actors (or not performed at all) and values close to one indicate a strong unidirectionality for a given behaviour. Third, we performed matrix correlation tests for both the absolute (R-test: Dietz, 1983) and relative (Rr-test: Hemelrijk, 1990) reciprocity of aggression; i.e. animals return exactly the amount of aggression they receive from each opponent (absolute reciprocity) vs. animals roughly return aggression, but following a hierarchical order based on who attacks them more (relative reciprocity). A positive correlation implies reciprocity in aggression and a negative correlation indicates overall asymmetries in aggression. Matrix correlation tests were conducted in the SOCPROG 2.6 software package (Whitehead, 2009).

Statistical analyses

In order to determine the stability of dominance scores over the study period, we computed the intraclass correlation coefficient (ICC(1,1)). This statistic quantifies how consistent the measures from an individual-typical case were at different opportunities (MacLennan, 1993), meaning in our case how consistent the NDS were from a given coati over the four periods. Values range between 0 and 1 with values close to 1 indicating highly consistent measures.

We used a linear mixed model (LMM) in order to assess the influence of individual dominance status (i.e. categorised as top-, middle- or low-ranked scores) on the short-term stability of ordinal rank (i.e. the

number of positions a given animal moved upwards or downwards the dominance hierarchy between consecutive periods). Status was assigned on the basis of an individual's ordinal rank during the first of the periods compared. Unbalanced status categories were defined based on a visual exploration of the data, later confirmed by our analyses, as it suggested that two small subsets of animals lay consistently at the top- and low-four positions of the hierarchy. Animals' identities and the number of opportunities each individual had for a rank change (i.e. repeated observations) were included as random effects, and an heterogeneous AR(1) covariance structure was set (Littell et al., 2000). To conduct pair-wise comparisons among the three levels of the categorical fixed effect and minimize the likelihood of type I error (Cohen et al., 2003), the LSD method (Carmer & Swanson, 1973) was employed. To further investigate the results of this model, we built a post-hoc LLM including the same random effects and covariance structure as above, but with the three consecutive periods when rank change was possible (i.e. early to late dry season, dry to rainy season, early to late rainy season) as the only categorical fixed-effect.

We built four generalized estimating equations models (GEE) – an extension of the generalized linear model (Liang & Zeger, 1986) – to evaluate the influence of reported seasonal variation in food resources on the general characteristics of coati conflicts. In each GEE model, the individual identities and behavioural sampling period (i.e. repeated measures) were introduced as subject and within-subject variables, respectively. For all these models, an autoregressive working correlation structure was selected along with a robust model-based estimator (Hardin & Hilbe, 2013). We defined the 1) rate of conflicts per hour, and the percentage of conflicts involving 2) contact aggression, 3) counter aggression, and 4) coalitionary support as the response variable in the corresponding GEE model. Because these response variables were continuous, and presented non-negative values with a point mass at zero (see Dunn & Smyth, 2005), we employed a tweedy probability distribution with a log-link function. Since our sampling period extended over the two climatic seasons occurring at the study site, we defined climatic season (dry season: February to May vs. rainy season: June to early October) as the only fixed effect in all these models.

Because anthropogenic food sources may have affected the patterns of coati agonistic behaviour, we built two post-hoc GEE models with the same subject and within-subject variables, and autoregressive working correlation, described previously. For these two models, the average number of tourists (if any) observed within a radius of ~ 20 m of the focal animal at the start and end of the behavioural sampling (a proxy for the availability of human-derived food items) was defined as the only fixed effect, and a negative binomial probability distribution with a log-link function was employed. The number of conflicts of any type occurring during each focal sampling, as well as the number of conflicts over anthropogenic food, were defined as response variables in the corresponding model.

Another GEE model was built in order to assess the influence of sex, age class, adult-young units (i.e. primary social bonds), and involvement in coalitions on individuals' dominance ranks. Subject and within-subject variables were the same than in the GEE models mentioned above, as well as the working correlation structure and robust model-based estimator. NDSs were included as the response variable and an identity link function was set. Then, a main effects model was built with sex (i.e. male or female), age class (i.e. juvenile, subadult, and adult), size of the adult-young unit, and participation in coalitions as fixed effects. We followed a frequentist rather than a model selection approach (sensu Mundry, 2011) since we were focused on testing the prediction that age, sex, subunit size, and coalitions structure coatis' dominance relationships. To avoid bias in parameter estimates and before running the model, we looked for the existence of multicollinearity in the predictors by computing the tolerance and variance inflation factor (Freckleton, 2011).

In order to test the effect of belonging to a particular adult-young unit on the individual NDS (in contrast with only the size of the adult-young unit affecting NDSs), we built a post-hoc GEE model with the same characteristics described previously, but having the identity of the adult-young unit (named after the corresponding adult female) as the only categorical fixed effect. Here we employed a Bonferroni adjustment method for taking into account the multiple contrasts performed among the five levels of the fixed effect (Cohen et al., 2003).

Because our prediction assumed that belonging to a larger adult-young unit represented more opportunities to form coalitions and acquire/maintain dominance rank, we built a GEE model (same subject and within-subject variables) with individuals' involvement in coalitions as the response variable, and the size of the adult-young units to which those individuals belonged as the only fixed effect. A negative binomial probability distribution with a log-link function was defined for this model.

Unless stated otherwise, the statistical analyses were carried out in SPSS 22 (IBM Corp, Armonk, NY, USA), tests were two-tailed, and significance was set at $p \le 0.05$.

Results

Coati conflicts and dominance hierarchy

An average of 3.35 conflicts per hour were observed during the whole study period with just 10% of these aggressive exchanges involving contact, and counter-aggression occurred in only in 5% of observations. One in ten conflicts involved coalitionary support (see Table 1 for a breakdown of the characteristics of these conflicts). We did not find effects of seasonality either on the rate of conflicts per hour (GEE: n=89, Wald chi-square= 1.374, df=1, p=0.241), or in the percentage of conflicts involving counter aggression (GEE: n=89, Wald chi-square= 0.005, df=1, p=0.942) or coalitionary support (GEE: n=89, Wald chi-square= 0.330, df=1, p=0.566). However, contact aggression was more common during dry season (February to May) relative to rainy season (June to early October) (GEE: n=89, Wald chi-square= 8.536, df=1, p=0.003, df=1, df

(Table 1 here)

We found a linear dominance hierarchy across each of our four observation periods (Table 2), with linearity and steepness values being lowest during the early dry season (Figure 1a; Table 2) and late rainy season (Figure 1d; Table 2), and highest during the late dry season (Figure 1b; Table 2) and early rainy season (Figure 1c; Table 2). The lower linearity and steepness values occurred during the two periods with the highest number of undecided relationships (up to 53% of all relationships, see Table 2). Because undecided relationships may affect negatively both linearity and steepness of hierarchy (Klass & Cords, 2011), we also computed these parameters for the whole dry and rainy seasons to increase the number of agonistic conflicts analysed per period (thus breaking ties for some dyads and avoiding zeros for other ones). Then, we found

that the number of undecided relationships decreased to a maximum of 15.81 %, and linearity and steepness values improved in both periods (Table 2).

To highlight the importance of coalitions in defining dominance relationships, but mainly because it represents the standard approach followed by most of the studies on this phenomenon, we also computed dominance parameters based exclusively on dyadic conflicts (i.e. excluding coalitions). This procedure changed the rank order, increased the number of undecided relationships, and decreased the linearity and steepness of the dominance hierarchy (Table S7). However, the main results were consistent with our previous analyses: linearity and steepness of the hierarchies were moderate but statistically significant during late dry season and early rainy season, and both parameters increased their values during the complete dry and rainy seasons, as the number of undecided relationships decreased. Furthermore, RO and AP stood as the most dominant individuals through the study period, and the two adult males were consistently ranked among the lowest five individuals.

(Table 2 and Fig. 1 here)

The asymmetries in the direction of aggression closely followed the variation observed for dominance hierarchy's parameters: aggression was more equitably exchanged when the linearity and steepness of dominance hierarchy were lower (i.e. early dry and late rainy seasons), and more unidirectional when these parameters reached their highest (i.e. late dry and early rainy seasons, see Table 3).

(Table 3 here)

Stability of dominance ranks

Individual dominance scores showed moderate repeatability over our four observation periods (ICC(1,1)= 0.702, 95% C.I.= 0.523–0.847, F(20,63)= 10.414, p < 0.001; Figure 2), and variation in ranks was influenced by individuals' dominance status (LMM: n= 66, F(2,20.65)= 6.167, p= 0.008), with middle ranked animals experiencing larger rank changes than top-ranked animals (Mean difference in ranks = 3.727, df= 20.69, p= 0.004, 95% C.I.= 1.323–6.131; Figure 2). Middle ranked animals also experienced larger but non-significant rank changes than low ranked animals (Mean difference in ranks= 2.371, df= 20.69, p= 0.053,

95% C.I.= -0.033–4.776). The period of observation did not affect the degree of rank variation observed (LMM: n = 66, F(2,30.54) = 0.943, p = 0.401).

367 (Fig. 2 here)

Age-sex classes, adult-young units and involvement in coalitions

Based on grooming patterns, 92.86% of all the juveniles and subadults (n=14) were associated to an adult female (see Table S1), resulting in five adult-young units of different sizes (see Figure 3). Whilst we did not find any significant effect of sex (GEE: n= 89, Wald chi-square= 0.267, df= 1, p= 0.606) or age class (Wald chi-square= 2.327, df= 2, p= 0.312) on dominance rank, the size of the adult-young unit to which animals belonged did positively and significantly predict their dominance scores; i.e. the largest the adult-young unit an individual belonged the more dominant it was (Wald chi-square= 6.522, df= 1, p= 0.011, B \pm S.E.= 0.203 \pm 0.079, 95% C.I.= 0.047–0.359). Certain adult-young units were dominant over others (GEE: n= 69, Wald chi-square= 49.662, df= 4, p \leq 0.001; Figure 3). The size of the adult-young units was positively and significantly associated with individuals' involvement in coalitions: the largest the adult-young unit an individual belonged the more it participated in coalitions (GEE: n= 69, Wald chi-square= 9.811, df= 1, p=0.002, B \pm S.E.= 0.185 \pm 0.059, 95% C.I.= 0.069–0.300). In turn, animals' involvement in coalitions also was positively and significantly related to their dominance scores: the more an individual participated in coalitions the more dominant it was (GEE: n= 89, Wald chi-square= 13.722, df= 1, p \leq 0.001, B \pm S.E.= 0.071 \pm 0.019, 95% C.I.= 0.034–0.109).

383 (Fig. 3 here)

Discussion

Dominance has been widely studied in very different taxa (e.g. Insecta, Mammalia) and using theoretical models. It represents a fundamental social phenomenon whose biological importance goes beyond its role in shaping social systems, also affecting developmental processes, life histories, and decision-making (Wilson, 1980; Pereira & Kappeler, 1993; Broom et al., 2009; King et al., 2008; Smith et al., 2010). Therefore, a careful evaluation of dominance is essential in order to assess the structure of animal societies

(*sensu* Hinde, 1976), but also for pinning down the constraints it imposes on individuals' opportunities and strategies to reach biological goals.

Coati species (*Nasua spp.* and *Nasuella spp.*) offer valuable models for understanding the factors shaping female social relationships. Although coatis have been the target of continuous interest among animal behaviourists for more than 50 years (e.g. Ingles, 1957; Kaufman, 1962), only one study (Hirsch, 2007) has properly addressed dominance (i.e. presenting metrics) in one species (*N. nasua*) of this clade. Here, we have quantified the characteristics of agonistic conflicts and the resulting structure of dominance/subordination networks among one band of free-ranging white-nosed coatis (*N. narica*), and discuss each of our major findings in turn.

Agonistic conflicts in this band were characterized by low percentages of contact aggression and scarce counter-aggression. This was unexpected, since patterns of mild aggression and moderate power asymmetries (see below) should minimize the potential costs from conflict escalation for subordinates and relax constraints for counterattacking (Matsumura, 1999). However, negative consequences from escalation not only arise from opponents' power asymmetries (e.g. risk of injuries) as aggression can impose non-obvious physiological and social costs on individuals involved (see Aureli et al., 2002). Frequent counteraggression would imply that opponents assume and impose further costs from conflict escalation, which actually is the opposite of what we found in this band. Even those conflicts involving coalitions or contact aggression usually lasted just a few seconds, and never resulted in opponents suffering visible wounds/injuries. A similar pattern of short and mild agonistic interactions has been reported among wild (Kaufman, 1964) and captive (Smith, 1977) white-nosed coatis (for ring-tailed coatis see Hirsch, 2007).

The general characteristics of coati conflicts may represent a conflict management mechanism based on low-cost behaviours (i.e. non-contact aggression) and escalation avoidance (i.e. rare counter-aggression), aimed to quickly settle the conflicts, minimize the costs from aggression, and preserve the benefits from sociability. This is a plausible explanation since coati species are strongly characterized by their prosocial behaviour. Behavioural mechanisms for preventing or buffering the social costs from aggression are expected when animals gain benefits from their sociopositive relationships (Kummer, 1979; Aureli & de Waal, 2000; Aureli & Schaffner, 2007) and do not experience a strong reproductive skew (see Kutsukake & Clutton-

Brock, 2008). In fact, coati bands are reported to contain multiple breeders (Gompper, 1995) and exhibit some degree of cooperative nursing (McToldridge, 1969; Russell, 1983), coalitionary support (Gompper et al., 1997; Romero & Aureli, 2008, Hirsch, 2007), and strong mother-offspring bonds (Kaufmann, 1962; Gompper et al., 1997; Romero & Aureli, 2007, 2008; Hirsch et al., 2012). In addition, high within-band relatedness characteristic of coati bands (Gompper et al., 1997; Hirsch et al. 2012) should limit the intensity of aggression, as severe aggression/escalation in this context may impose costs on inclusive fitness (de la O & Mondragón-Ceballos, 2014), especially considering coatis' powerful claws and sharp teeth.

Dominance parameters reflect the general characteristics of coati conflicts. This band formed a network of dominance relationships (sensu Preuschoft & van Schaik, 2000), mainly characterized by their moderate linearity and steepness. Both parameters were relatively stable over time and remained at mid-levels even when they were expressed at their strongest. Despite the large number of undecided relationships during the first and last observational periods, which are predicted to negatively affect linearity and steepness (Klass & Cords, 2011), these parameters remain statistically significant at every period. Computing dominance parameters for the whole dry and rainy seasons – to include more conflicts evaluated per dyad – resulted in a drastic decrease of undecided relationships and the improvement of linearity and steepness, although both remained at moderate levels. When coalitions were excluded, the large increase in undecided relationships negatively affected dominance parameters, but we still found moderate linearity and steepness in the dominance hierarchy when < 40% of all relationships were undecided (see Table S7). Furthermore, alternative measures of power asymmetry at the group level reflected linearity and steepness outcomes, revealing both moderate imbalances and limited reciprocity in aggressive exchanges, regardless of the observation period. Therefore, our results are likely to describe accurately the dominance structure of this band (see Wittemyer & Getz, 2007; Klass & Cords, 2011).

The shallow dominance gradients observed here imply that most of the coatis were unable to exert a strong negative influence (e.g. coercion) on others (see Henzi & Barrett, 1999), making a strict orderliness of the hierarchy unlikely over long periods. Our results are in line with this prediction: most of the instability in the dominance hierarchy arose from the intermediate positions, where power asymmetries among animals were subtle. In contrast, more stability was found when looking at the opposite extremes of the hierarchy:

high-ranked animals were mostly the same anytime and low-ranked individuals had only a small scope for improving their status, with low-ranked coatis hardly ever rising to intermediate and never to top positions for more than one period. Together, these results revealed a moderate despotism in coati dominance.

Unidirectional signals indicating the dominance/subordination status between individuals (i.e. formal dominance, de Waal, 1986) are not predicted when power asymmetries among individuals are low (as we found), and the likely outcome of agonistic encounters is relatively uncertain (Preuschoft & van Schaik, 2000). Moreover, coati prosocial behaviours mentioned above should confer subordinates some influence on dominants (i.e. leverage: Hand, 1986), making unnecessary explicit signals of subordination to gain tolerance (Preuschoft & van Schaik, 2000). As expected, we did not observe interactions suggesting formalised dominance relationships in this band, neither have such signals been reported in previous studies of coati behaviour (e.g. Kaufmann, 1962; Smith, 1977; Gompper et al., 1997; Hirsch, 2007; Romero & Aureli, 2008). In addition, computing dominance hierarchies based on the direction of grooming interactions did not reveal any transitivity (i.e. linearity) in these exchanges, with a large number of dyadic relationships remaining undecided (Table S8).

In contrast to ring-tailed coatis (*N. nasua*) in Iguazú, Argentina (Hirsch, 2007), dominance in this band of white-nosed coatis (*N. narica*) was not structured by the sex or age class of animals. However, it is worth noticing that the two adult males associated with the band ranked consistently at the bottom of the hierarchy. Smith (1977) described a similar situation among captive white-nosed coatis: after one male and various females were housed together, the male behaved increasingly submissive towards females and finally avoided their hostile proximity. It is possible that our small sample size (four males and only two of them adults), hampered our ability to find a significant effect of sex on rank. Further studies are necessary to determine how common and enduring is the association of males to white-nosed coati bands, and the cost/benefits from that.

Rather than sex or age classes, adult-young units and coalitions structured dominance relationships in this band. The size of the adult-young unit an individual belonged to was positively associated with its dominance scores; i.e. the more close-associates an animal had the more dominant it was. Such subunits may or may not represent close-kin bonds (e.g. mother-offspring, elder sister-young), but they can be viewed as

functionally similar in terms of providing the main source of social support during development, and even later in lifetime. For example, the top-four individuals in the dominance hierarchy belonged to the largest adult-young unit (n= 7), with the adult female holding the alpha position. This suggests that the availability of potential allies in the band may directly affect the opportunities to improve social rank, maybe via kin support. Among the white-nosed coatis of Barro Colorado, Panama, those individuals with close relatives in the band received more coalitionary support than those without (Gompper et al., 1997). Similarly, in our studied band those animals from larger adult-young units also participated more in coalitions. Furthermore, we found that those individuals more involved in coalitions also attained higher dominance scores.

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Dominance relationships appeared to be more loosely defined when data on coalitionary support were not taken into account (cf. Table 2 vs Table S7). In fact, coalitions play a fundamental role in defining dominance relationships (e.g. Primates: Watts, 2010; Carnivora: Smith et al., 2010), by introducing a source of power asymmetry beyond individual attributes ("intrinsic" vs "derived dominance"; see review in Watts, 2010). Coalitions are also a central element of coati agonistic conflicts (Gompper et al., 1997; Romero & Aureli, 2008, Hirsch, 2007), and in this band they made up 10% of all observed conflicts. Such percentage is noticeably lower than the previously reported 68% for free-ranging N. narica (Gompper et al., 1997) and 38% for captive N. nasua (Romero & Aureli, 2008), but more similar to that reported by Hirsch (2007) at 7% for free-ranging N. nasua and within the average values reported by Smith et al. (2010) for 16 non-primate species ($\bar{x} \pm \text{S.D.} = 17 \pm 8\%$). Moreover, > 60% of the observed coalitions in this band involved individuals from the same adult-young unit, which may be close-relatives: e.g. mother and offspring, siblings (see Hirsch & Maldonado, 2011, who accurately determined mother-offspring relationships based on grooming bouts; also see Romero & Aureli, 2008). Such sources of coalitionary support (i.e. kin) would be even more important if a proportion of the remaining ~ 40% of coalitions teaming up individuals from different adultyoung units might involve more distant relatives (e.g. grandmothers, aunts, elder siblings), which would be expected if support provides inclusive fitness benefits (Hamilton, 1963). Jointly, the regular occurrence of coalitions among (but not exclusively) members of the same adult-young unit, and the positive influence of subunit size and coalitions on dominance scores, raises the possibility of a 'loose' nepotism characterizing coati dominance style. We employ the term 'loose nepotism' because: a) kinship among those subunits was uncertain, and b) the resulting hierarchy was not strictly organized in a sequence of adult-young units whose

members ranked consecutively, nor did individuals within adult-young units follow the Kawamura's (1958) 'youngest ascendancy rule' (i.e. 'strong nepotism'). Once again, it is possible that the moderate and dynamic differences in winning success, particularly among mid-ranked individuals, preclude the development of a 'strongly nepotistic' dominance style, including larger bias in coalition formation.

Our results broadly fit our prediction on the dominance characteristics (i.e. moderate despotism, mild agonist conflicts) expected on the basis of coati diet (i.e. fruits and invertebrates) and the associated modes of foraging competition (i.e. contest and scrambling, respectively). However, our results did not provide support for the prediction that dominance parameters vary in response to regular climate oscillations (i.e. dry and rainy season), a proxy for the main type of competition the animals were likely to face in response to expected food distribution. Linearity and steepness were both weakly and moderately expressed within the same season, and the alternative measures of power asymmetry did not suggest any influence of weather on the pattern of agonistic interactions. Neither the rate of conflicts per hour, nor the percentage of conflicts involving counter-aggression or coalitions varied significantly through time, and only the percentage of contact aggression followed our predicted relationship (see below). However, note that the presumed spatiotemporal patterns of food distribution were largely uncertain, since we did not estimate systematically the abundance or the consumption of food by coatis throughout the year.

Instead, our results suggest that variation in coati dominance was more likely influenced by the stages of reproductive season: mating, gestation, and nesting. Indeed, contact aggression was more common during the dry season, but this was particularly noticeable at the time of mating season (see Table 1) when the dominance hierarchy was also more poorly defined (see Table 2). In primates increased severity of aggressive patterns has been reported when animals face more uncertainty in dominance relationships (e.g. de Waal, 1982; Gust & Gordon, 1991; McCowan et al., 2008). Moreover, the most linear and asymmetric dominance relationships occurred during gestation and nesting periods. Here, it is possible that the energetic demands of pregnancy and nursing (Speakman, 2008) have intensified contest competition among females, as suggested by the slight increment in the frequency (although not in the severity) of agonistic conflicts at that time (see Table 1). Alternatively, the increase of linearity and steepness may have resulted from the socio-cognitive development of juveniles (i.e. the gradual acquisition of knowledge of the social rules governing group life).

In this case, more well-differentiated and stable dominance relationships can be expected as young animals became older. In fact, there was a trend towards more asymmetric and transitive dominance relationships whilst juveniles approached 1 year of age, and this trend disappeared when the new cubs (socially inexperienced but strongly supported by adults; see Gompper et al., 1997; Hirsch, 2007) joined the band. However, the number of positions that animals moved in the dominance hierarchy between consecutive periods (i.e. our proxy for rank stability) did not significantly change over time.

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Even though different in terms of the variables structuring dominance (age class and sex vs. social support), our results are similar to those reported by Hirsch (2007) for ring-tailed coatis regarding linearity of the dominance hierarchy, regular occurrence of coalitions, and rare use of contact aggression during agonistic conflicts. We extended the description of coati dominance style by providing data on despotism (i.e. steepness, aggression direction) and potential nepotism (i.e. interrelationship among adult-young units, coalition involvement, and dominance scores), and also on the general features of agonistic conflicts. None of the evaluated aspects of coati dominance were expressed strongly anytime, and dominance relationships were noticeably less despotic and stable than they are in other animal societies largely structured by female kinship (e.g. cercopithecines: Di Fiore & Rendall, 1994; spotted hyaenas, Crocuta crocuta: Frank, 1986; Holekamp & Smale, 1991). The observed patterns of power asymmetries between individuals – in spite of their large differences in resource holding potential (e.g. experience, size, weight) - and mild aggression during agonistic conflicts resembled the characteristics of an egalitarian dominance style (Hand, 1986; Isbell & Young, 2002). On the other hand, the hierarchical organization of dominance relationships (and their very existence), the moderate bias in aggression direction, the regular occurrence of coalitions, and the positive effects of primary social bonds and coalitions on dominance scores denote some degree of despotism-nepotism in dominance structure. Actually, coatis showed most of the characteristics (i.e. female philopatry, mild aggressive patterns, coalition formation, potential kin effects on individual rank, moderate linearity and steepness of dominance hierarchy) which define the resident-nepotistic-tolerant dominance style (Sterck et al., 1997) and their equivalent behavioural syndromes (see Isbell & Young, 2002; Clutton-Brock & Janson, 2012); such low amounts of counter-aggression during agonistic conflicts were contrary to that predicted for a tolerant style (Thierry, 2000; Balasubramaniam et al., 2012). Further data on post-conflict affiliations would be beneficial in order to situate coati species in the tolerance-intolerance continuum.

It is worth noticing that between group contest competition (BGC) has been proposed as the main selective pressure in the evolution of resident-nepotistic-tolerant societies (see Isbell & Young, 2002; Clutton-Brock & Janson, 2012). In this regard, Kaufmann (1962) described infrequent and mild conflicts among bands of wild white-nosed coatis in Barro Colorado, Panamá. Similarly, Hirsch (pers. comm.) observed low amounts of BGC among ring-tailed coatis in Iguazú National Park, Argentina. In the present study BGC accounted for 9% of all agonistic conflicts observed during dry season, but was barely observed during the rest of the time. Almost all the instances of BGC took place between the two bands described in Methods section (i.e. our studied band and the second one). We cannot make further conclusions from such a limited sample, but the role of BGC in shaping coati social relationships seems limited. Nonetheless, BGC may be more evident at higher population density and its effects on sociability more suitable of being studied.

Human activities at the study were likely to affect the agonistic interactions of this band. In fact, coati dominance relationships showed more despotism (but still at moderate levels) when conflicts over anthropogenic food sources were more frequent (Tables 2 and 3). Although our analyses revealed that the frequency of coati conflicts increased as the number of visitors in the surroundings was higher (our proxy for the availability of anthropogenic food), there is not a direct relationship between the number of visitors and the frequency of conflicts occurring over human derived food items. Feeding animals is forbidden at the site and most visitors followed authorities' guidelines, but not all of them. Which visitors would feed the animals was random, and therefore largely unpredictable for coatis. Thus, it is possible that coati expectancies on anthropogenic food availability in response to touristic influx decreased social tolerance in general, but not enough to promote strong despotism in dominance relationships.

We acknowledge that studying a single coati band imposes limitations on our discussion. Also contextual (e.g. perturbed habitat) and methodological (e.g. indirect estimates on food abundance and consumption, correlational results) issues should be considered to avoid risky generalizations at the species level or about the general factors determining dominance relationships. However, we consider that our study offers a plausible evaluation of coati dominance structure, but also possess a heuristic value. Our results suggest that under certain ecological circumstances, the traditional view of white-nosed coatis living in an egalitarian society (see Kaufmann 1962, Smith 1977, Gompper 1995, Gompper et al. 1997) might not be the

case. Because anthropogenic disturbance is a growing situation around the world, and coatis have been reported to regularly display activities around urbanised areas/touristic sites (e.g. Hirsch, 2009; Sazima, 2010; Ferreira, 2013; de la Rosa-Arana et al. 2016), our results may reflect a common situation faced for other coati populations.

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Overall, whilst our results did not match exactly any of the dominance styles predicted by socioecological models (see Isbell & Young, 2002; Clutton-Brock & Janson, 2012), we consider the singularities of coati dominance may arise from two key aspects of coati life history largely different from primates: a) the number of offspring produced per reproductive event, and b) the life span. Indeed, whilst most of the primates are characterized by producing only one young per reproductive event and being relatively long-lived (Harvey et al., 1987; Ross, 1998; Jones, 2011), coati females can produce up to six cubs per reproductive event and have a shorter life span (Gompper, 1995). As a result of this, reproductive adult females raise multiple cubs simultaneously, facing the challenge of making them becoming fully independent before the next reproductive season (i.e. < 1 year). On the other hand and similar to primates, coati species (Nasua spp.) are plural breeders (Gompper, 1995; Gompper & Decker, 1998), which produces a social situation where multiple juveniles from different mothers are born into the band simultaneously. At least two consequences on the ontogeny of coati dominance relationships are expected from the aforementioned: first, coati mothers face a scenario where they have to divide their attention and agonistic support among various equally related individuals (and differentiate them from the other same-age ones), making a strict adherence to the 'youngest ascendance' order (Kawamura, 1958) observed among despotic-nepotistic species impossible (e.g. Macaca spp., see Chapais, 2004). In addition, coati life expectancy and accelerated growing rate are likely to impose strong constraints on the time and opportunities for socio-cognitive development and expression of complex social behaviour.

Our results support the claim that dominance represents a continuum of power imbalances within relationships (Hand, 1986) which accounts for its basic properties: egalitarianism-despotism, tolerance-intolerance, individualism-nepotism (Klass & Cords, 2015). Although it has been proposed these dimensions tend to covariate in a specific way (the systematic variation hypothesis: Castles et al., 1996) and constitute dominance styles (see Balasubramaniam et al., 2012), we consider it better not to assume a priori the

existence of a close association between the components of dominance phenomenon. It is now important for more comparative studies on dominance and other aspects of sociability (i.e. bonding, cooperativeness) among carnivores and other mammals to provide valuable elements to assess how ecological, life history and phylogenetic factors participate in the variation of different aspects of sociality between and within species and populations.

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Table 1. Characteristics of coati agonistic conflicts across the study period for n=23 white-nosed coatis.

Average values computed from the whole dataset.

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		%	%	%	%	%	
Period	Conflicts/Hr ^a	Contact aggression ^{b,c}	Counter- aggression ^{b,d}	Coalitions ^{b,d}	Undecided conflicts ^{b,d}	Conflicts over ASF ^{b,d}	T@SS
Feb-Mar	2.60	17.28	1.69	9.80	39.19	3.67	25.67
Apr-May	3.16	11.84	2.70	8.28	31.25	12.84	34.58
Jun-Jul	4.16	8.45	6.48	11.20	40.94	28.04	45.53
Aug-Oct	2.72	7.44	6.96	10.44	40.51	8.25	48.40
Average	3.35	10.43	4.82	10.07	37.92	17.41	41.86

ASF= Anthropogenic sources of food (e.g. peanuts, chips, food waste)

T@SS= Number of tourist at the start of scan samplings

938 ^a Computed from focal samplings only

^b Computed from focal and ad libitum samplings

^c Relative to all instances of aggression

941 d Relative to all conflicts

943 **Table 2.** Dominance parameters (Corrected Landau *h*', Steepness) across the study period for n=23 white-944 nosed coatis.

Period/Season	Corrected Landau h'	<i>p</i> -value	Steepness	Right p-value	% undecided relationships
Feb-Mar	0.251	0.007	0.109	< 0.001	52.81
Apr-May	0.387	< 0.001	0.262	< 0.001	23.32
Dry season ^a	0.431	< 0.001	0.319	< 0.001	15.81
Jun-Jul	0.439	< 0.001	0.326	< 0.001	15.15
Aug-Oct	0.299	< 0.001	0.162	< 0.001	45.89
Rainy season ^b	0.540	< 0.001	0.405	< 0.001	9.09

945 ^a February to May

947

946 b June to early October

Table 3. Silk's Reciprocity Index (RI), directional consistency index for aggression (DCI), Dietz R-test, and Hemelrijk Rr-test (with respective *P* values for the latter two) across the study period for n=23 white-nosed coatis.

Period	RI $(\overline{x} \pm S.D.)$	DCI $(\overline{x} \pm S.D.)$	Dietz R-test (absolute reciprocity)	p-value (R-test)	Hemelrijk Rr-test (relative reciprocity)	p-value (Rr-test)
Feb-Mar	0.672 ± 0.339	0.377 ± 0.472	0.227	< 0.001	0.268	< 0.001
Apr-May	0.569 ± 0.328	0.580 ± 0.459	0.363	< 0.001	0.284	< 0.001
Jun-Jul	0.438 ± 0.333	0.638 ± 0.421	0.267	< 0.001	0.161	< 0.001
Aug-Oct	0.597 ± 0.369	0.459 ± 0.490	0.461	< 0.001	0.153	< 0.001

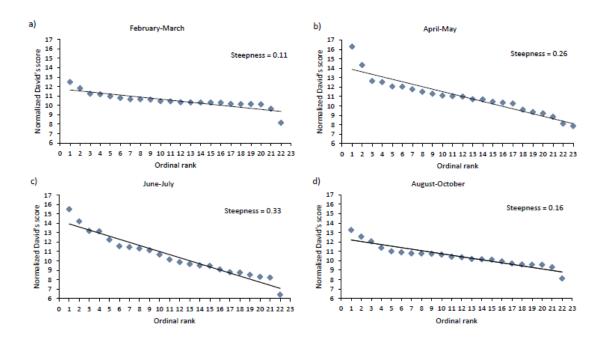


Figure 1. Dominance ranks (normalised David's scores) as a function of ordinal rank for n=23 white-nosed coatis across four observation periods: a) middle dry season/mating season, b) late dry season/gestation period, c) early rain season/birthing and nesting period, d) late rainy season/new litters become part of the group. Steepness of the hierarchy is represented by the slope of the regression line.

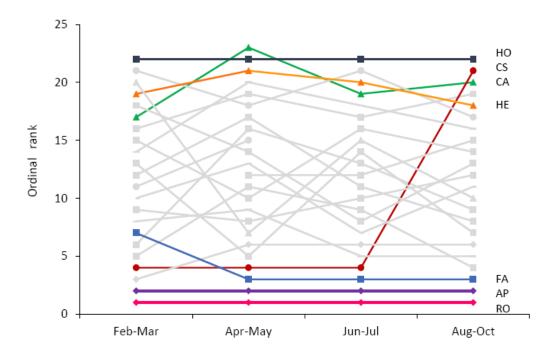


Figure 2. N=23 coatis' ordinal rank across four observation periods. Animals ranked at the top (n=4) and bottom (n=3) positions of the dominance hierarchy are most stable and are represented by coloured lines. Capital letters at the right of the graph represent these animals' ID codes. First and last ordinal numbers correspond to the alpha and omega animals, respectively.

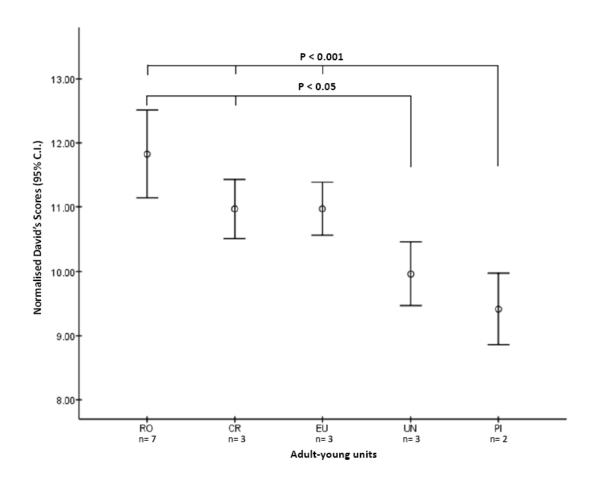


Figure 3. Differences in dominance (Normalised David's Scores) among five adult-young units, assumed from observed affiliative grooming patterns.

SUPPORTING INFORMATION Resident-nepotistic-tolerant dominance style in wild white-nosed coatis (Nasua narica) Claudio de la O^{1,2}, Ines Fürtbauer¹, Andrew J. King¹, David Valenzuela-Galván² ¹Department of Biosciences, College of Science, Singleton Park, Swansea University, Swansea SA2 8PP, UK ²Centro de Investigación en Biodiversidad y Conservación, Universidad Autónoma del Estado de Morelos, Universidad 1001, Colonia Chamilpa, Cuernavaca, Morelos 62209, México

Table S1: White-nosed coati band age-sex class composition, adult-young units defined from grooming data (and named after the adult female), and focal samples conducted.

ID Code	Sex	Age class	Adult-young unit	No. focal samples
AP	3	Juvenile ^a	RO	46
BR	9	Juvenile ^a	RO	47
CA	3	Adult ^c		44
CL	9	Juvenile ^a	UN	45
CR	9	Adult ^c	Head of unit	50
CS	9	Subadult ^b	RO	50
DE	9	Adult ^c		42
DI	9	Subadult ^b	PI	51
ES	9	Juvenile ^a	CR	47
EU	\$	Adult ^c	Head of unit	42
FA	\$	Juvenile ^a	RO	46
HE	\$	Adult ^c		43
НО	3	Adult ^c		38
MA	\$	Subadult ^b	RO	47
NA	\$	Juvenile ^a	EU	11
PAN	3	Juvenile ^a	EU	44
PE	\$	Subadult ^b	RO	48
PI	\$	Adult ^c	Head of unit	49
RO	9	Adult ^c	Head of unit	47
SE	9	Juvenile ^a		42
TA	9	Juvenile ^a	CR	47
UN	9	Adult ^c	Head of unit	42
UNC	2	Juvenile ^a	UN	41

⁹⁸⁹ 990

Q = female

^{991 ♂ =} male

^{992 &}lt;sup>a</sup> Juvenile < 1y.o.

⁹⁹³ b Subadult < 2y.o.

^{994 °} Adult > 2y.o.

Table S2: Behavioural definitions.

Category	Behaviour	Definition								
Affiliation	Grooming	The giver gently "handles" the fur of the target, mainly by using its muzzle and rarely its paws. It could be unidirectional or mutual.								
	Retreating	Moving back or walking away from a former aggressor.								
Submissive	Fleeing	The animal runs away from a former aggressor which is chasing after it.								
Submissive	Displacement	Spontaneously avoiding an approaching individual (i.e. a non-former aggressor) by stepping aside or walking away.								
	Nose-up display	A conspicuous threat at the opponent by exposing the incisors and canines.								
Non-contact aggression	Feinting	A quick head movement at a close target, the muzzle slightly open and exposing subtly the incisors and canines.								
	Lunging	Running towards the opponent who could either move or stay.								
	Chasing	Running after a fleeing opponent for more than 3 m.								
	Rough contact	Approaching and making a brusque contact at the opponent's body.								
	Pushing	Using the head or forepaws to drive off a group mate in close proximity.								
Contact aggression	Biting	Exerting pressure on some part of the opponent body by employing the aggressor tooth, mainly the maxillary canines.								
aggression	Fighting	A brief but conspicuous encounter where the opponents grabbed each other employing their claws, rolled together on the ground, and exchanged bites.								
Agonistic support	Coalition	Two or more animals joining forces to attack/ defend another individual. Individuals forming a coalition could either initiate the attack/defence simultaneously, or the supporter(s) could "join in" after a few seconds.								

Table S3: Win-loss sociomatrix for n= 22 white-nosed coatis during February-March period. Individuals in ID column are ordered according to their ordinal rank in this period (from top to the bottom). Conflicts won against each opponent are presented in rows.

AYU	Age/Sex	ID	RO	AP	EU	CS	CR	BR	FA	ES	PAN	PE	NA	MA	DE	ΡI	UN	CL	CA	SE	HE	TA	DI	НО
RO	AF	RO	X	2	0	2	1	0	2	5	1	1	0	2	1	0	3	1	1	3	2	0	5	2
RO	JM	AP	0	X	0	1	0	3	4	5	0	2	0	1	1	0	0	1	1	0	3	1	1	4
EU	AF	EU	0	0	X	1	0	0	0	1	1	1	0	1	0	2	1	0	0	0	0	0	2	2
RO	SAF	CS	0	1	0	X	0	0	0	0	1	2	0	2	0	0	0	0	3	1	1	1	2	1
CR	AF	CR	0	0	1	0	X	0	0	0	0	1	0	0	2	2	1	0	0	0	0	0	0	0
RO	JF	BR	0	1	0	1	0	X	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1
RO	JF	FA	1	0	0	0	0	0	X	4	0	1	0	1	0	0	0	0	0	4	0	1	0	2
CR	JF	ES	0	0	1	1	0	0	2	X	0	0	0	1	0	0	0	0	0	2	0	1	2	6
EU	JM	PAN	0	0	1	0	0	0	0	0	X	0	3	0	0	0	1	3	2	0	0	0	0	3
RO	SAF	PE	0	1	0	0	0	0	1	0	0	X	0	1	0	0	0	1	1	0	0	1	0	0
EU	JF	NA	0	0	0	0	1	0	0	0	1	0	X	0	0	1	1	1	0	0	0	0	1	2
RO	SAF	MA	0	0	0	0	0	0	0	1	1	0	0	X	0	1	0	0	1	0	0	0	1	2
-	AF	DE	1	0	0	0	0	0	0	0	0	0	0	0	X	0	0	0	2	1	0	1	0	0
PI	AF	PΙ	0	0	0	0	0	0	0	0	0	0	1	0	1	X	0	0	1	0	0	0	0	4
UN	AF	UN	0	0	1	0	1	0	0	0	0	0	0	0	0	0	X	0	0	0	0	0	0	0
UN	JF	CL	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	X	0	0	0	0	1	0
-	AM	CA	3	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	X	1	0	0	4	10
-	JF	SE	0	2	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	X	1	0	0	2
-	AF	HE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	0
CR	JF	TA	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	X	0	0
PI	SAF	DI	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	2	0	0	0	X	2
	AM	НО	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	X

1008 AF= Adult female

1009 AM= Adult male

1010 SAF= Subadult female

1011 JF=Juvenile female

1012 JM= Juvenile male

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Table S4: Win-loss sociomatrix for n= 23 white-nosed coatis during April-May period. Individuals in ID column are ordered according to their ordinal rank in this period (from top to the bottom). Conflicts won against each opponent are presented in rows.

AYU	Age/Sex	ID	RO	AP	FA	CS	DE	EU	TA	PAN	ES	UN	CR	UNC	PE	SE	NA	BR	MA	DI	CL	ΡI	HE	НО	CA
RO	AF	RO	X	7	1	6	4	3	2	5	2	3	8	1	3	3	2	6	1	4	3		10	1	3
RO	JM	AP	2	X	4	3	2	0	6	2	5	0	3	0	2	3	1	7	3	2	1	4	0	1	1
RO	JF	FA	0	2	x	3	0	0	1	0	1	2	2	0	0	1	0	2	2	1	0	1	1	2	1
RO	SAF	CS	2	0	0	X	0	1	0	1	3	3	3	1	3	2	1	1	2	5	0	3	1	2	4
-	AF	DE	1	0	0	2	x	0	2	2	1	1	0	3	0	0	0	0	0	1	2	2	1	0	4
EU	AF	EU	0	0	0	0	0	X	2	1	1	3	1	1	0	0	1	0	0	1	1	2	4	1	4
CR	JF	TA	0	3	3	0	0	0	X	3	0	1	0	0	3	2	0	1	1	0	1	2	1	0	1
EU	JM	PAN	0	0	2	0	0	1	1	X	1	1	2	5	0	0	3	0	1	1	2	1	1	2	4
CR	JF	ES	0	0	1	3	3	2	0	0	X	0	1	0	0	2	0	1	0	1	0	1	2	3	3
UN	AF	UN	1	0	0	2	1	0	0	0	2	X	0	2	2	1	1	1	0	2	2	3	0	3	1
CR	AF	CR	0	0	0	0	4	1	2	3	1	1	X	1	0	1	1	0	2	0	2	0	5	4	0
UN	JF	UNC	0	1	0	1	0	0	2	1	0	0	1	X	1	1	0	0	0	1	1	1	2	0	2
RO	SAF	PE	0	0	0	0	2	0	1	0	0	0	0	1	X	0	0	0	1	2	0	0	3	0	1
-	JF	SE	2	0	0	1	0	0	0	0	1	0	3	0	0	X	0	2	2	2	0	0	1	1	4
EU	JF	NA	0	0	1	0	1	0	0	1	0	0	0	0	0	0	X	0	0	1	1	0	0	0	0
RO	JF	BR	2	1	0	2	0	1	0	0	1	0	1	0	0	2	0	X	1	0	0	1	0	0	0
RO	SAF	MA	0	1	0	0	0	0	0	1	0	0	0	0	1	2	0	1	X	3	1	0	0	0	0
PI	SAF	DI	0	0	0	0	0	0	0	0	0	2	0	1	0	0	1	1	2	X	3	1	1	1	5
UN	JF	CL	0	0	0	0	0	0	0	3	1	1	3	1	0	0	1	1	0	1	X	0	0	3	0
PI	AF	PI	0	1	0	0	1	1	0	1	0	1	0	1	0	0	0	1	0	0	1	X	2	1	0
-	AF	HE	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	X	2	1
-	AM	НО	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	X	7
_	AM	CA	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	1	1	0	1	X

1021 AF= Adult female

1022 AM= Adult male

SAF= Subadult female

JF=Juvenile female

JM= Juvenile male

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Table S5: Win-loss sociomatrix for n= 22 white-nosed coatis during June-July period. Individuals in ID column are ordered according to their ordinal rank in this period (from top to the bottom). Conflicts won against each opponent are presented in rows.

AYU	Age/Sex	ID	RO	AP	FA	CS	ES	EU	PE	SE	CR	PAN	MA	UNC	BR	DE	TA	UN	CL	ΡI	CA	HE	DI	НО
RO	AF	RO	X	5	8	7	4	8	3	8	5	3	1	2	2	5	9	7	4	4	3	12	10	2
RO	JM	AP	3	X	5	2	8	2	3	14	3	5	3	0	7	0	5	1	2	1	2	0	6	0
RO	JF	FA	2	1	X	2	2	0	1	4	5	0	4	1	1	1	2	3	2	0	5	4	3	7
RO	SAF	CS	2	1	3	X	2	2	1	2	5	3	2	3	0	3	1	2	5	1	1	4	4	3
CR	JF	ES	2	1	1	2	X	3	0	4	0	1	3	0	4	6	0	4	1	2	5	4	9	6
EU	AF	EU	0	0	0	4	0	X	0	0	3	6	2	0	1	0	0	0	3	2	3	7	1	2
RO	SAF	PE	0	1	0	0	0	1	X	0	0	2	0	0	1	2	1	1	0	1	2	5	2	2
-	JF	SE	3	2	2	6	1	0	2	X	1	1	3	0	2	1	0	1	0	2	5	6	4	3
CR	AF	CR	2	0	0	3	4	1	1	0	X	1	1	3	1	5	1	4	1	0	4	5	8	1
EU	AM	PAN	0	1	0	2	2	2	0	2	4	X	3	3	3	0	0	0	1	0	4	2	2	3
RO	SAF	MA	0	1	0	0	2	0	0	3	0	0	X	2	0	2	0	2	2	3	0	1	3	0
UN	JF	UNC	1	1	1	0	0	1	0	1	0	0	0	X	0	2	1	0	0	0	0	1	1	7
RO	JF	BR	1	0	0	0	1	0	0	3	3	0	1	0	X	1	3	0	1	1	2	1	3	2
-	AF	DE	1	1	1	0	0	0	1	1	1	1	0	0	1	X	0	1	0	0	1	1	0	0
CR	JF	TA	0	0	2	0	0	0	0	2	1	0	0	0	0	1	X	0	0	1	0	1	0	3
UN	AF	UN	0	0	0	0	0	0	0	0	1	0	0	2	2	1	0	X	1	0	1	2	0	2
UN	JF	CL	2	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	X	0	0	0	1	6
PI	AF	PΙ	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	X	2	1	0	0
-	AM	CA	1	0	1	0	2	2	0	2	0	4	1	1	2	0	0	0	0	1	X	1	1	1
-	AF	HE	1	1	0	0	2	0	1	0	1	3	0	3	2	0	1	0	0	0	3	X	0	1
PI	SAF	DI	0	0	0	2	2	0	0	0	1	3	0	1	0	0	3	1	2	4	0	0	X	0
	AM	НО	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	X

1034 AF= Adult female

1035 AM= Adult male

SAF= Subadult female

1037 JF=Juvenile female

1038 JM= Juvenile male

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Table S6: Win-loss sociomatrix for n= 22 white-nosed coatis during August-October period. Individuals in ID column are ordered according to their ordinal rank in this period (from top to the bottom). Conflicts won against each opponent are presented in rows.

AYU	Age/Sex	ID	RO	AP	FA	CR	ES	EU	DE	MA	BR	TA	PE	PAN	SE	UN	UNC	ΡI	DI	HE	CL	CA	CS	НО
RO	AF	RO	X	4	3	1	2	1	1	1	1	0	3	0	2	2	0	6	1	2	3	1	4	0
RO	SAM	AP	0	X	1	2	2	0	0	0	2	1	4	0	1	1	0	2	2	0	1	1	2	5
RO	SAF	FA	1	0	X	1	1	1	0	2	3	0	4	0	0	0	0	1	0	2	0	0	3	2
CR	AF	CR	0	0	0	X	1	0	0	0	0	0	1	1	0	0	0	0	2	0	2	0	2	1
CR	SAF	ES	2	0	0	0	X	0	0	0	2	0	1	0	0	2	0	1	3	1	0	0	5	3
EU	AF	EU	0	0	0	0	0	X	0	1	0	0	0	1	0	2	0	1	0	0	0	4	0	0
-	AF	DE	0	0	0	0	0	0	X	0	1	0	0	0	0	0	2	0	0	0	2	1	0	0
RO	AF	MA	0	0	0	0	0	0	0	X	0	0	0	1	0	0	1	0	2	2	0	3	0	2
RO	SAF	BR	1	0	0	0	1	0	0	0	X	1	0	0	0	1	0	0	0	0	0	0	0	4
CR	SAF	TA	0	1	0	0	0	0	0	0	0	X	0	0	0	1	0	0	1	0	0	1	2	1
RO	AF	PE	0	0	0	0	0	1	0	0	0	0	X	0	0	0	0	1	1	2	1	0	0	2
EU	SAM	PAN	0	0	0	0	1	0	1	1	0	0	0	X	0	0	1	0	7	1	1	5	2	1
-	SAF	SE	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	0	0	0	0	1	1	1
UN	AF	UN	0	0	0	0	0	0	0	0	0	0	0	1	0	X	0	1	0	0	1	2	0	0
UN	SAF	UNC	0	0	0	0	0	0	0	0	0	0	0	1	0	0	X	2	0	0	0	1	0	2
PI	AF	PΙ	0	0	0	0	0	0	0	1	0	0	0	5	0	0	1	X	0	0	2	1	1	5
PI	AF	DI	0	0	0	0	1	0	0	0	0	1	0	2	1	0	1	0	X	0	1	1	1	2
-	AF	HE	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	X	0	0	1	0
UN	SAF	CL	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	X	0	1	0
-	AM	CA	0	0	0	0	1	0	0	0	0	0	0	4	0	2	0	3	1	1	0	X	0	0
RO	AF	CS	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	4	0	0	X	1
_	AM	НО	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	X

1047 AF= Adult female

1048 AM= Adult male

SAF= Subadult female

1050 SAM= Subadult male

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Table S7: Dominance parameters (Corrected Landau h', Steepness) across the study period for n=23 whitenosed coatis. Conflicts involving coalitionary support were excluded from these analyses.

Period/Season	Corrected Landau h'	<i>p</i> -value	Steepness	Right p-value	% undecided relationships
Feb-Mar	0.162	0.284	0.058	0.047	64.93
Apr-May	0.359	< 0.001	0.200	< 0.001	37.15
Dry season ^a	0.357	< 0.001	0.245	< 0.001	28.06
Jun-Jul	0.295	0.003	0.223	< 0.001	27.70
Aug-Oct	0.209	0.094	0.088	< 0.001	59.74
Rainy season ^b	0.380	< 0.001	0.293	< 0.001	18.18

^a February to May ^b June to early October

1074 Table S8: Dominance parameters (Corrected Landau h', Steepness) across the study period, based on 1075 grooming interactions among n=23 white-nosed coatis.

Period/Season	Corrected Landau h'	<i>p</i> -value	Steepness	Right <i>p</i> -value	% undecided relationships
Feb-Mar	0.141	0.384	0.028	0. 931	80.24
Apr-May	0.138	0.388	0. 051	0. 967	68.77
Dry season ^a	0.143	0.310	0.062	0.0691	62.05
Jun-Jul	0.160	0.247	0.051	0.849	69.70
Aug-Oct	0.136	0.431	0.026	0.560	80.09
Rainy season ^b	0.183	0.147	0.074	0.054	61.47

^a February to May ^b June to early October