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Research article

Inter-specific interactions involving *Lemur catta* housed in mixed-species exhibits in UK zoos

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Abstract

Ring-tailed lemur *Lemur catta* are a popular Madagascan species kept in zoos due to their appeal to visitors. As a flagship endangered species, they are often used to highlight conservation messages and are frequently kept in mixed-species and walk-through exhibits providing an immersive experience for the public. However, agonistic events may be more frequent in exhibits housing multiple territorial primate species with differing dominance hierarchies. Observations were undertaken in nine UK zoos housing a total of 105 *L. catta* in 10 polyspecific exhibits using 'all occurrence sampling' to record frequency and duration of agonistic and affiliative interactions between *L. catta* and other species of lemur. Observations were conducted in two-hour continuous periods under two conditions: when food was presented by keepers and when this was not the case. The presence or absence of provisioned food did not predict changes in any of the relationships examined. Overall, agonistic inter-specific interactions were observed slightly more frequently than affiliative interactions; the difference was not significant. Analysis revealed that there was a significant difference in both the frequency and duration of inter-specific affiliative and agonistic interactions between some exhibits, the presence of infants (aged <1 year old) and single sex exhibits significantly predicted an increase in the frequency of affiliative interactions whereas larger troops and the absence of infants were associated with a reduction of agonistic events. This study found that the conditions within individual exhibits (including group and design characteristics) significantly influenced interactions between *L. catta* and other lemur species. The findings suggest implications for ongoing captive care, and specifically for the management of species age/combinations.

Introduction

Ring-tailed lemur *Lemur catta* are a popular Madagascan species kept in zoos due to their appeal to visitors. As a flagship endangered species, they are often used to highlight conservation messages (*Andriaholinirina* et al. 2014) and are frequently kept in mixed-species and walk-through exhibits providing an immersive experience for the public. However, agonistic events may be more frequent and/or intense in exhibits housing multiple territorial primate species with differing dominance hierarchies. *L. catta* live in female-bonded primate groups where females are philopatric and establish kin relationships to protect 'clumped' resources from competitors (Isbell and Overdorff 2008). As a result, the presence of food (including its abundance and distribution) can influence inter- and intra-group relationships significantly (Isbell 1991) and may lead to increased aggression in captive contexts (Law 2018). Prolonged and intense aggression in captivity due to resource competition can result in chronic stress, compromising both physical and psychological health (Kutsukake and Castle 2001; Kutsukake 2003; Dalton and Buchanan-Smith 2005). Observation of such inter-specific interactions can provide insight into the nature of relationships between species and their compatibility for shared housing (Wojciechowski 2004; Leonardi et al. 2010; Casares et al. 2011) and a better understanding of the benefits (increased social complexity and enrichment) and risks of polyspecific housing of specific species (Pearson et al, 2010; Buchanan-Smith et al. 2013).

The frequency of intra-specific agonistic behaviour across lemur species has been documented as low (Ellwanger 2002; Roeder et al. 2002a;b; Saucier 2008). Most aggression displayed by *L. catta* appears to be dyadic, with little intervention from other individuals and generally most 'spats' are often brief and do not involve serious physical contact resulting in injury (Jolly 1966). However, 'high level', injurious and sometimes fatal events associated with targeted aggression and infanticide of individuals has been recorded in wild and captive populations (Vick and Pereira 1989; Pereira 1993; Digby 1999; Sauther et al. 1999; Jolly et al. 2000; Palagi et al. 2005; Kittler and Dietzel, 2016). Male-male aggression also becomes intense during the breeding season (Jolly 1966; Cavigelli and Pereira 2000; Parga and Henry 2008; Wilson and Hanlon, 2010). Although agonistic behaviour may look very similar in many lemurs (Vick and Conley 1976), it is affected by species, dominance relationship and the presence of young (Pereira et al. 1990; Nakamichi and Koyama 2000; Roeder et al. 2002a;b). It includes signals such as 'hard stare', 'grunt', 'spat call', 'lunge', 'chase'; displacement and contact such as 'cuffing', 'grasping' and 'biting' (Roeder et al. 2002a; Palagi et al. 2005).

Affiliative behaviours (including reconciliation behaviours) reinforce bonds, facilitate relationship repair and reduce further conflict (Koyama 2001; Wahaj et al. 2001; Ellwanger 2002; Palagi et al. 2005). Post-conflict affiliative behaviour in *L. catta* is documented as a two-phase process (Rolland and Roeder 2001), with increased proximity 10 min after an agonistic event and affiliative interactions towards the victim within the following hour (Palagi et al. 2005). Affiliative behaviour displayed by *L. catta* includes huddling, greeting (naso-nasal, face grooming), allogrooming and olfactory investigation/sniffing of nose and genitals (Pereira and Kappeler 1997). Sitting or resting in proximity (<1 m) is considered evidence of kinship and bonding in primate species (Gould 1996; 1997; Ellwanger 2002; Marolf et al., 2007; Farine et al. 2016; Ren et al. 2018).

Many of the species housed with *L. catta* are geographically separated from them in the wild but occupy similar ecological niches and lifestyles (Curtis et al. 1999; Ellwanger 2002; Vasey 2003; Erkert and Cramer 2006; Mittermeier et al. 2010; Razafindramanana 2011; Nadhuro et al. 2016; Tecot et al. 2016; Valenta et al. 2016; Guthrie et al. 2017); it is plausible that this co-housing may lead to inter-specific conflicts which could compromise their welfare (Thomas and Maruska 1996; Dalton and Buchanan-Smith 2005). Analysis of interactions between *L. catta* and other lemurs housed in 10 UK exhibits was conducted to investigate the extent of inter-specific agonistic and affiliative behaviour and establish relationship characteristics. Competition (e.g., during feeding) may impact the frequency of agonism and reconciliation exhibited by all lemurs within an exhibit. To investigate potential impact on captive lemur welfare three specific hypotheses were tested: (1) Inter-specific agonistic interactions are significantly more frequent than inter-specific affiliative interactions as *L. catta* are often housed with allopatric species with whom they do not associate and may compete for resources within the exhibit; (2) Inter-specific agonistic interactions are significantly more frequent and longer in duration during feeding due to competition and increased proximity; and (3) Frequency of inter-specific agonistic interactions will be significantly different between *L. catta* and *Varecia* species, from that between *L. catta* and *Eulemur* species as agonism between *L. catta* and *Varecia* species has been documented in captivity (Gecewicz 2001; Ziegler 2002; Manna et al. 2007; Taylor, 2009).

Method

Observations were undertaken in nine UK zoos (Table 1, anonymity was granted during recruitment) housing a total of 105 *L. catta* in 10 polyspecific exhibits with one zoo having two exhibits (Exhibits 4 and 5).

Observation sampling

L. catta were observed under two conditions: when food was presented by keepers and when this was not the case. For each condition, the observation periods were conducted for two continuous hours each day over 5 days per enclosure (see Table 2 for ethogram). The two recording periods were separated by one hour and always occurred during visiting hours. 'Food' observations were scheduled to commence when the keeper entered the exhibit for feeding. The zoo's feeding schedule dictated when the four hours of observation could be conducted. All occurrence sampling (Martin and Bateson 2007) was used to record frequency and duration of visible incidences of agonistic and affiliative interactions between *L. catta* and other species of lemur, during each condition. Other parameters recorded included the species of the initiator of interactions and are detailed below. In total, 20 hours of observation (over 5 days) were made at each exhibit, totalling 200 hours of observation across all 10 exhibits.

The size and complex nature of many of the exhibits meant that some individuals were out of view at times. When *L. catta* groups separated, the observer prioritised observation of the larger group of individuals still 'in view'. To reduce observer effect (Stamp-Dawkins 2007) and to encourage habituation by animals the observer took position 30 min before sampling commenced.

Data analysis

The number of *L. catta* housed in each exhibit varied; therefore, data were standardised for statistical analyses. The total frequency and duration of each interaction for each group of *L. catta* was divided by the number of *L. catta* housed in the exhibit, to calculate frequency and duration of interaction per ring-tailed lemur. For analysis of agonistic and affiliative interactions between *L. catta* and specific species, the data were standardised for the number of exhibits in which each specific species of lemur was housed. ANOVA tests were used to investigate differences in frequency and duration of interactions between exhibits (Field 2009). Multiple Linear Regression models (Field 2009) were used to test for management factors which predicted frequency and duration of interactions (see Table 3 for predictors used).

Results

Feeding events did not predict changes in inter-specific interactions (R^2=27.4%, Adjusted R^2=25.3%, F=0.52, P=0.819) (Law 2018). Thus, for analysis of type of interaction and differences between exhibits and species, the data from these two conditions were combined.

Overall, agonistic inter-specific interactions were observed slightly more frequently than affiliative interactions (3.47±5.67 and 3.08±4.86, mean and SD, respectively) over 20 hours, but not significantly so (t=−0.23, P=0.596). Non-contact aggression occurred most frequently, followed by proximity (Figure 1). In terms of duration, there was a significant difference between affiliative (15.77±18.3 min, mean and SD) and agonistic (0.12±0.17 min, mean± and SD) inter-specific interactions per *L. catta* over 20 hours (t=3.83, P<0.001). Proximity was the inter-specific interaction with the longest duration (25.16 min per lemur, per 20 hours, ±32.87 SD), followed by huddling (4.42 min, ±9.51 SD) (Figure 2).

Frequency and duration of interactions in each exhibit

ANOVA revealed that there was a significant difference in both the frequency (Agonistic, F(9,10)=54.45, P<0.001; Affiliative, F(9,10)=4.19, P=0.018) and duration (Affiliative, F(9,10)=70.06, P<0.001) of inter-specific affiliative and agonistic interactions

Table 1. Species, enclosure and sampling summary for the study zoos.

Zoo exhibit	Number of *L. catta*	Sex of *L. catta*	Other species housed		Month sampled	Breeding season (mating or birth)	Infants (<1 year) present	Exhibit characteristics	Year sampled
			Name	Number					
EX1	24	Male only	*Varecia rubra* *Eulemur rufus*	2 2	January	N/A	N	Exhibit type: Walkthrough Size category: >200 m^2 Feeding strategy: Scatter feeding	2013
EX2	4	Mixed sex	*Varecia rubra* *Eulemur rufus* *Eulemur rubriventer*	2 4 2	April	Birth	Y	Walkthrough Size category: >200 m^2 Feeding strategy: Scatter feeding	2013
EX3	23	Mixed sex	*Eulemur rubriventer* *Eulemur albifrons*	2 3	May	Birth	N	Exhibit type: Walkthrough Size category: >200 m^2 Feeding strategy: Scatter feeding	2013
EX4	6	Male only	*Eulemur rufus*	2	July	N/A	N	Exhibit type: Non-walkthrough Size category: >200 m^2 Feeding strategy: Scatter feeding	2013
EX5	7	Male only	*Eulmur rufus* *Varecia variegata*	1 2	July	N/A	N	Exhibit type: Non-walkthrough Size category: >200 m^2 Feeding strategy: Scatter feeding	2013
EX6	9	Male only	*Eulemur macaco* *Eulemur collaris* *Varecia variegata*	2 4 3	October	N/A	N	Exhibit type: Walkthrough Size category: >200 m^2 Feeding strategy: Scatter/hand feeding	2013
EX7	10	Mixed sex	*Varecia rubra*	3	January	Out of season	N	Exhibit type: Non-walkthrough (visitors allowed entry for 30 min per day during keeper talk/feed) Size category: 150–200 m^2 Feeding strategy: Scatter/hand feeding	2014
EX8	8	Mixed sex	*Eulemur mongoz* *Eulemur rubriventer*	2 2	February	N/A	N	Exhibit type: Walkthrough Size category: 150–200 m^2 Feeding strategy: Scatter feeding	2014
EX9	9	Male only	*Eulemur macaco*	2	April	N/A	N	Exhibit type: Walkthrough Size category: 150–200 m^2 Feeding strategy: Scatter feeding	2014
EX10	5	Mixed sex	*Eulemur rufus*	3	August	N/A	N	Exhibit type: Walkthrough Size category: >200 m^2 Feeding strategy: Scatter feeding	2014

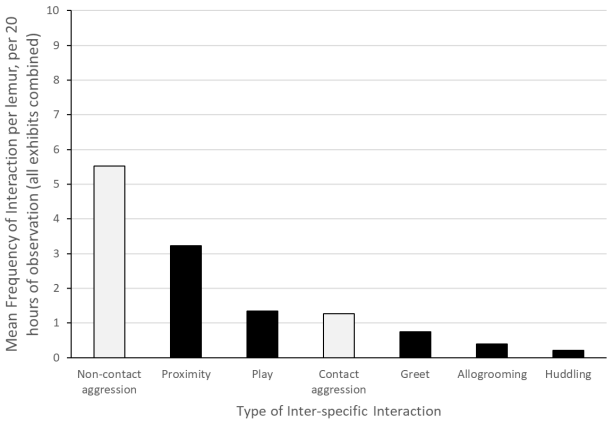

Figure 1. Mean frequency for different types of inter-specific interactions per ring-tailed lemur. Black bars represent affiliative interactions, grey bars represent agonistic interactions.

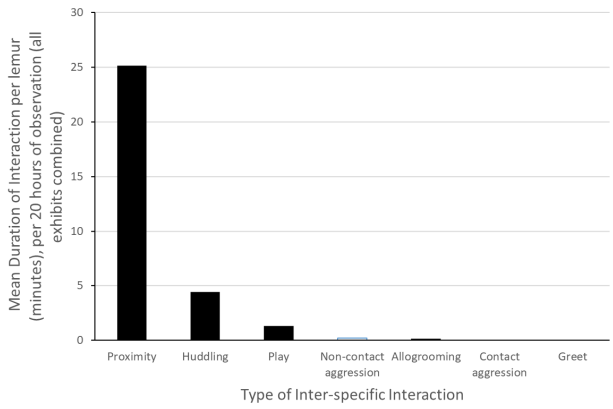

Figure 2. Mean duration for different types of inter-specific interactions per ring-tailed lemur. Black bars represent affiliative interactions, grey bars represent agonistic interactions.

Table 2. Ethogram of *L. catta i*nter-specific interactions.

Intention	Name	Description
Agonistic interactions	Contact aggression	Grabbing/grasping, cuffing, biting, slapping or wrestling (accompanied with bared teeth and vocalisation)
	Non-contact aggression	Chasing, lunging, swinging limb at another (without making contact), accompanied with threatening facial expression such as bared teeth and vocalisations including grunting or 'spat call'
Affiliative interactions	Huddling	Resting in a hunched position with their tail tucked around the body whilst maintaining contact with one or more lemurs
	Close proximity	*L. catta* sit within 1 metre of another species for more than 10 seconds omitting instances that fall within the other categories
	Allogrooming/Solicit grooming	Two or more individuals (*L. catta* and another species) engage in grooming each other using tooth comb or grooming claw/individual presents a body part or adopts posture next to another individual (different species) followed by grooming
	Sniff/nose touch	An individual places its nose near another's body, sniffs another lemur or touches their nose (between *L. catta* and other species)
	Social play	Non-aggressive interaction between *L. catta* and other species involving, grab, chase or wrestling
Vocalisations	Intergroup call	Vocalisations which involve the whole/majority of *L. catta* and those of a different species, not in conjunction with any of the other behaviours

between some exhibits. Post hoc analysis (Dunnett T3 unequal variances) was conducted for pairwise comparisons (see Figure 3). The frequency and duration of inter-specific affiliative interactions was higher in Exhibit 2 compared to the majority of the other exhibits.

Effects of various management factors on frequency and duration of interactions

The presence of infants (aged <1 year old) and single sex exhibits significantly predicted an increase in the frequency of interspecific affiliative interactions whereas larger troops of *L. catta* and the absence of infants were associated with a reduction of agonistic events (Table 4). The factors that significantly predicted the duration of affiliative interactions between *L. catta* and other lemurs are shown in Table 4. However, neither feeding events nor the genera housed with *L. catta* resulted in significant predictions regarding frequency or duration of either interaction type (R^2=27.4%, Adjusted R^2=25.3%, F=0.52, P=0.82).

Aggression between species

In half of the exhibits *L. catta* acted as the aggressors more often than any other species (Figure 4); however, Kruskal Wallis H test showed no significant difference in how frequently they acted as the aggressor towards any specific other lemur species (H=12.90, P>0.05). *L. catta* were most frequently agonistic towards *V. rubra*; however, 93% of this agonism was recorded in one exhibit (EX2) where two elderly individuals were targeted. This is discussed in more detail elsewhere (Law 2018).

Data on the frequency of agonistic interactions between *L. catta* and other lemur species is shown in Table 5. The mean frequency

Table 3. Management factors included in the multiple linear regression models for frequency and duration of inter-specific interactions.

Predictor Name	Description
Genera	The genus to which the species of lemur housed with *L. catta* belong
Number	Number of lemur species housed with *L. catta*
Food condition	Feeding event versus no food
Exhibit type	Walkthrough versus non-walkthrough
Exhibit size	Outdoor area categorised as either 100–150 m^2, 150-200 m^2 or >200 m^2
Troop size	Number of *L. catta* housed in the exhibit, categorised as: <15, 15–26, >26
Sex	Mixed-sex groups versus bachelor groups
Presence of infants	Presence of *L. catta* aged <1 year old

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Table 4. Summary of Multiple Linear Regression Model results testing for management factors (see Table 3) reporting on those factors which significantly predicted the frequency (per *L. catta*) or duration of *L. catta* interactions with individuals from other lemur species (per 20 hours of interactions, number per hour in brackets). Note. * predictors with significant level p <0.05; Adjusted R^2 >50% shows a large effect size according to Cohen (1988); B = unstandardized regression coefficient; SE_B = Standard error of the coefficient; ß = standardized coefficient'

Dependent variable	Predictor	Effect	R^2 (%)	Adjusted R^2 (%)	F value	P value	B	SE_B	ß
Frequency of inter-specific affiliative interactions	Presence of infants	Decrease of 10.3 (0.52) events in exhibits where infants were absent	71.5	50.7	F(8,11)=3.45	P=0.031	-10.239	2.810	-0.866*
	Sex composition	Increase of 6.8 (0.34) events in single sex exhibits					6.793	2.686	0.717*
Frequency of inter-specific agonistic interactions	Troop size	Decrease of 7.6 (0.38) events in exhibits with larger troop size (15–26 individuals)	76.2	58.9	F(8,11)=4.41	P=0.013	-7.583	3.436	-0.549*
	Presence of infants	Decrease of 11.8 (0.59) events in exhibits where infants were absent					-11.844	2.993	-0.858*
Duration of inter-specific affiliative interactions	Number of species housed with L. catta	Increase of 1370.34 (68.52) seconds as the number of lemur species housed with L. catta increased	96.2	89.9	F(5,15)=20.65	P<0.001	22.839	2.678	0.958*
	Exhibit size	Decrease of 1821.6 (91.08) seconds in larger exhibits					-30.360	4.295	-0.780*
	Troop size	Decrease of 1479.18 (73.96) seconds in exhibits with larger troop size (15–26 individuals)					-24.653	3.650	-0.553*
	Presence of infants	Decrease of 2634.06 (131.70) seconds in exhibits where infants were absent					-43.901	4.639	-0.985*
	Sex composition	Increase of 2434.38 (121.72) seconds in single sex exhibits					40.5013	4.413	1.136*

of agonism between *L. catta* and *Varecia* species was higher than that between *L. catta* and *Eulemur* species, but not significantly so (Mann-Whitney U=5.00, P=0.171).

Affiliative behaviour between species

Affiliative interactions varied for the species involved when several lemur species were co-housed with *L. catta* (Figure 5). Exhibits 4, 7, 9 and 10 are not included in Figure 5 as *L. catta* were only housed with one other lemur species; therefore, 100% of interactions occurred between the two groups housed in each of these locations (see Table 6 for total frequency of inter-specific affiliative interactions per zoo).

In Exhibit 1 and Exhibit 3, all the interactions occurred with just one of the species housed with *L. catta* (*E. rufus* and *E. albifrons*, respectively) and none with *V. rubra* and *E. rubriventer* respectively. In two of the three exhibits housing both *Varecia*

(a. Frequency)

Inter-specific affiliative interactions \ Inter-specific agonistic interactions	EX1	EX2	EX3	EX4	EX5	EX6	EX7	EX8	EX9	EX10
EX1		0.068	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EX2	0.006		<0.001	0.066	0.155	0.121	0.002	0.141	0.470	0.151
EX3	1.000	0.001		1.000	0.127	1.000	1.000	0.152	1.000	0.290
EX4	1.000	0.016	1.000		1.000	1.000	1.000	1.000	1.000	1.000
EX5	0.490	0.008	0.369	1.000		0.726	0.427	0.993	1.000	1.000
EX6	0.807	0.008	1.000	1.000	0.705		1.000	0.633	1.000	0.802
EX7	1.000	<0.001	1.000	1.000	0.224	1.000		0.500	1.000	0.886
EX8	0.024	0.011	0.346	1.000	0.999	0.124	0.209		1.000	0.999
EX9	0.303	0.011	0.063	0.592	1.000	0.464	0.035	0.948		1.000
EX10	0.900	0.004	1.000	1.000	0.992	0.999	1.000	1.000	0.906	

(b. Duration)

Inter-specific affiliative interactions \ Inter-specific agonistic interactions	EX1	EX2	EX3	EX4	EX5	EX6	EX7	EX8	EX9	EX10
EX1		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EX2	0.052		0.014	0.135	0.105	0.084	0.578	1.000	0.085	0.744
EX3	1.000	0.003		1.000	1.000	1.000	1.000	0.578	1.000	1.000
EX4	1.000	0.006	1.000		1.000	1.000	1.000	1.000	1.000	1.000
EX5	0.965	0.488	0.734	1.000		0.554	1.000	1.000	0.769	0.669
EX6	0.998	0.044	1.000	1.000	0.867		1.000	1.000	1.000	0.554
EX7	0.252	0.033	1.000	1.000	0.609	0.330		1.000	1.000	1.000
EX8	0.994	0.081	0.524	0.877	1.000	0.731	0.205		1.000	1.000
EX9	0.660	0.658	0.057	0.107	1.000	0.492	0.289	0.932		0.567
EX10	1.000	0.043	1.000	1.000	0.920	1.000	0.531	0.929	0.566	

Figure 3. P values for post hoc analysis for the two factors (a) 'frequency of inter-specific affiliative behaviour' (bottom left horizontal cells in white) and 'frequency of inter-specific agonistic interactions' (top-right vertical cells in grey) and (b) respective durations (affiliative in bottom left horizontal cells in white, all parametric, variances homogeneous), agonistic interactions in top-right vertical cells in grey. Note: significant P values (P<0.05) are shown in red bold for parametric analysis (Tukey), Bonferroni correction was applied.

Table 5. Frequency of inter-specific agonistic interactions between *L. catta* and other named species in all exhibits shared and the mean frequency of inter-specific agonistic interactions between *L. catta* and other named species per exhibit.

Species	Number of individuals of named species across the exhibits	Number of exhibits	Number of *L. catta* across the exhibits	Total frequency of Inter-specific agonistic interactions across the exhibits	Mean frequency of inter-specific agonistic interactions per exhibit
V. variegata	7	2	16	57	28.5
V. rubra	7	3	38	103	34.3
E. rufus	12	5	46	108	21.6
E. rubriventer	6	3	35	55	18.3
E. albifrons	3	1	23	0	0
E. macaco	4	2	18	3	1.5
E. collaris	4	1	9	1	1
E. mongoz	2	1	8	1	1

and *Eulemur* species with *L. catta*, more affiliative interactions were recorded with species from the *Eulemur* genus. The mean frequency of affiliative interactions between *L. catta* and *Varecia* species was lower than between *L. catta* and *Eulemur* species and approached significance (Mann-Whitney U=21.00, P=0.067).

Proximity was significantly more frequent than any other type of affiliative behaviour (Kruskal Wallis H test: H=14.573, P=0.006), accounting for 60% of all inter-specific affiliative behaviour (see Table 7). Inter-specific play was only observed with *E. rufus*; 34 of 41 play interactions (82.9%) occurred in Exhibit 2 and were associated with play between and with infants. Only two exhibits housed *L. catta* with *E. macaco*; 84.1% of all inter-specific affiliative interactions between the species were recorded in the exhibit at Exhibit 9.

Only one incidence of affiliative behaviour involving physical contact was recorded between *L. catta* and *Varecia* species; this was between *L. catta* and one *V. variegata* individual housed in Exhibit 5. The latter joined a group already huddled together for just over eight minutes. *E. mongoz* and *E. albifrons* did not engage in any affiliative interactions involving physical contact.

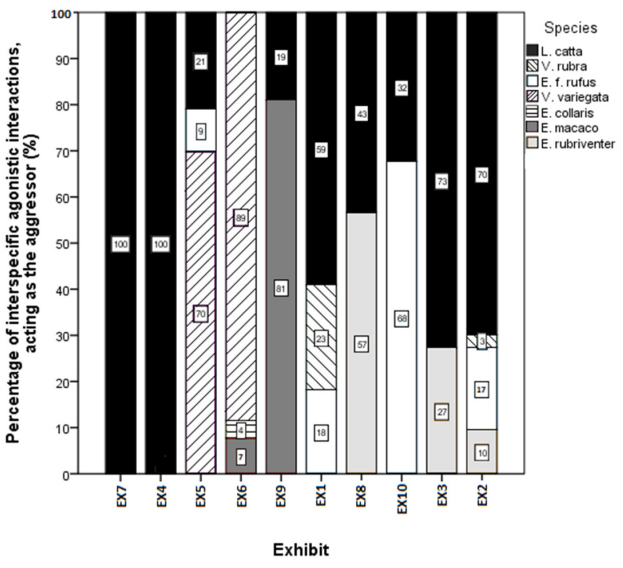

Figure 4. Species acting as aggressors in inter-specific agonistic interactions (as percentage), in each exhibit. *E. albifrons* (in EX3), *E. rufus* (in EX4), *E. mongoz* (in EX8) and *V. rubra* (in EX7) did not act as the aggressors in any of their interactions with *L. catta*.

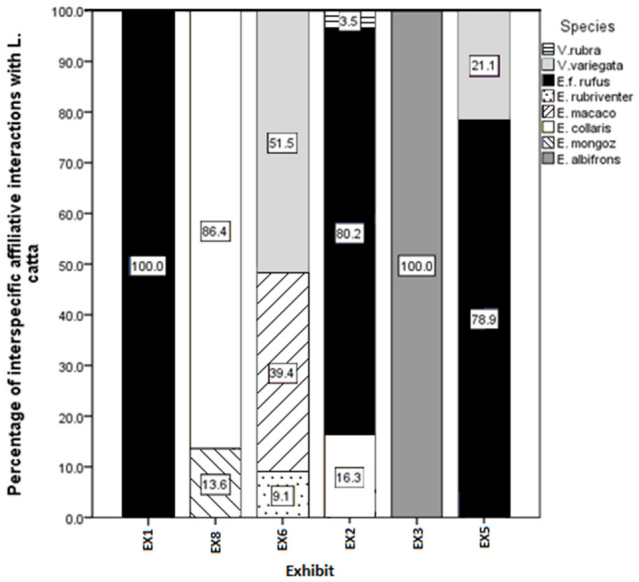

Figure 5. Percentage of inter-specific affiliative interactions involving L. catta, per species, for each exhibit.

Table 6. Total frequency of inter-specific affiliative interactions between *L. catta* and other species in each exhibit over 20 hours of observation.

Zoo Exhibit	Name of species co-housed with *L. catta*	Total number of affiliative inter-specific interactions
EX1	*Varecia rubra*	0
	Eulemur rufus	48
EX2	*Varecia rubra*	4
	Eulemur rufus	92
	Eulemur rubriventer	19
EX3	*Eulemur albifrons*	9
	Eulemur rubriventer	0
EX4	*Eulemur rufus*	8
EX5	*Eulemur rufus*	58
	Varecia variegata	16
EX6	*Eulemur macaco*	15
	Eulemur collaris	4
	Varecia variegata	20
EX7	*Varecia rubra*	5
EX8	*Eulemur mongoz*	7
	Eulemur rubriventer	44
EX9	*Eulemur macaco*	69
EX10	*Eulemur rufus*	27

Discussion

It might be indicative of negative impacts on welfare if agonistic interactions amongst lemurs housed in mixed exhibits are more frequent or last longer than reported within *L. catta* troops in single-species exhibits or between lemurs in the wild. Only anecdotal observations of interactions between captive *L. catta* and other lemurs have been published (Gecewicz 2001; Ziegler 2002; Manna et al. 2007; Taylor 2009). This study found that inter-specific interactions were infrequent, but when they occurred, proximity and non-contact aggression were observed most frequently.

Effects of management factors on inter-specific interactions between lemurs

Presence of food

Overall, the delivery of food from keepers did not significantly predict frequency or duration of either type of inter-specific interaction, suggesting that competition for food resources was not sufficiently intense to negatively affect the welfare of these ring-tailed lemurs. However, in Exhibit 10, 15 of the 21 agonistic interactions directed toward *L. catta* by a male group of *E. rufus* occurred during feeding times. This exhibit consisted of large areas of established trees and shrubs, simulating a deciduous woodland and the group of *E. rufus* only contained males. Ellwanger (2002) and Razafindramanana (2011) recorded the closely related *E. rufus* x *E. collaris* hybrid displacing *L. catta* from gallery forest into peripheral scrub areas and contact aggression directed towards *L. catta* individuals. *E. rufus* do not use a dominance hierarchy related to sex; therefore, males will challenge females (Ostner and Kappeler 1999; Jolly et al. 2000; Roeder et al. 2002b). It is possible that the group of male *E. rufus* in this exhibit were more willing to challenge this small mixed-sex group of *L. catta* for access to food and canopy, leading to higher incidences of aggression compared to other exhibits. Research on enclosure use, however, suggests scatter feeding is beneficial (Law 2018).

Number of species

Co-housing *L. catta* with species from either the *Varecia* or *Eulemur* genera did not predict frequency or duration of any inter-specific interactions significantly; however, as the number of species housed in the exhibits increased, so did the duration of inter-specific affiliative interactions. Proximity was the inter-specific affiliative interaction with the longest duration. It is possible that as the total number of species (and therefore individuals) housed

Table 7. Mean frequency of each type of affiliative interaction between *L. catta* and each lemur species (interactions per species, per number of exhibits where the named species are co-housed).

Species	Mean Frequency of Inter-specific Affiliative per Interaction Type				
	Proximity	Allogrooming	Huddling	Nose greet	Play
V. rubra	1	0	0	0	0
V. variegata	15.5	0	0.5	0	0
E. rufus	15.6	2.2	7.6	4.2	8.2
E. rubriventer	16.3	0	0	1	0
E. macaco	22.5	3.5	8.5	6.5	0
E. collaris	2	0	0	1	0
E. mongoz	6	0	0	0	0
E. albifrons	11	0	0	0	0

in the exhibit increased, they were forced to share space and thus be in closer proximity for longer. Only two exhibits included in the study housed three or more lemur species with *L. catta* and due to the small sample size, it is difficult to draw conclusions. Compared to the other exhibits, much higher rates of inter-specific affiliative interactions were recorded in Exhibit 2 where there were a lot of infants playing with other lemurs in the exhibit. In Exhibit 6, the *L. catta* were a bachelor group. Housing all male groups was associated with increases in inter-specific affiliative behaviour and decreases in agonistic behaviour (Table 4); the absence of females (often the aggressors in *L. catta* groups) may have been the cause of higher rates of affiliative interactions at this zoo.

It is unlikely that changes in the duration of affiliative interactions were associated merely with reconciliatory behaviour as increases in the number of species housed did not yield similar effects on inter-specific agonism. In the absence of further data, one might presume that this type of management does not pose a threat for the species' welfare. Further investigation of inter-specific interactions in more exhibits housing more than three lemur species is needed.

Sex composition

The frequency of affiliative interactions was higher in single-sex groups: all five such exhibits housed male bachelor groups. The dominance hierarchy within the male community remains relatively stable except during the mating season (Gould et al. 2005; Gould and Ziegler 2007; Parga 2009) when status reversals and challenges from low ranking males have been observed (Sauther 1991; Gould and Ziegler 2007; Parga et al. 2016). It is possible that conflict between males is less intense in the absence of females, leading to fewer behavioural stress effects (Gould et al. 2005; Wilson and Hanlon 2010). Similar findings were documented in both wild and captive bachelor groups of gorillas (Robbins 1995; Stoinksi et al. 2001). Recommendations for polyspecific housing within the current *L. catta* Husbandry Guidelines also suggest that housing bachelor groups in mixed-species exhibits can ease problems with aggression (Taylor 2009).

Presence of infants

Only one exhibit included in the current study housed infants less than one year old. Despite this, presence of young significantly predicted both frequency ($P=0.031$) and duration ($P<0.001$) of affiliative interactions and the duration ($P=0.013$) of agonistic interactions. It is unsurprising that females may display more protective behaviours when infants are present; agonistic behaviour associated with protection of young has been documented in both wild and captive contexts (Nakamichi and Koyama 2000; Charpentier and Drea 2013). It is interesting to note, however, that play behaviour was observed between *L. catta* infants and both young and adults of other species. It is possible that infants provide greater complexity within the environment and thus act as stimulation for adults of differing species. Which species may benefit from the presence of infants; however, requires further investigation before firm conclusions can be drawn regarding suitability of mixed-species housing for breeding groups; neither play or any other affiliative interaction beyond proximity were ever observed between the *V. rubra* individuals housed in this exhibit and any of the other species. Presence of infants may not, therefore, have provided a positive effect on individuals from the *Varecia* genus and exhibits like this warrant further attention.

Agonistic interactions

The mean frequency of inter-specific agonistic interactions was 3.47 events per ring-tailed lemur and total duration of agonism per ring-tailed lemur was just 7.2 sec over 20 hours of observation. Encouragingly, this is lower than reported for intra-specific agonism between *L. catta* housed in single-species exhibits (Sbeglia et al. 2010; Shire 2012; Law 2018). While frequencies of inter-specific agonistic interactions in captivity have not been published, Manna et al. (2007) described such interactions between *L. catta* and *V. variegata* as rare but did not record frequency or duration of interactions. Agonistic interactions have been observed at feeding sites between wild *L. catta* and an introduced *Eulemur* hybrid (Ellwanger 2002); however, *L. catta*, *E. collaris* and *P. verreauxi* maintained a peaceful co-existence in Ambatotsirongorongo, Madagascar (Razafindramanana 2011).

Whilst the low incidence and duration of aggression overall is encouraging, closer attention is warranted. *L. catta* were the aggressors during most of the inter-specific agonistic interactions observed; they were the most frequent aggressors in five of the exhibits during observation. The analysis did not present any clear explanation for this finding, nor the additional data gathered for the studies (Law 2018). Personality traits, the animals' history and other factors could be important and further research could explore this. Interactions varied with respect to the other lemur species involved. Also, it is worth noting that agonistic interactions tend to be short events. Therefore, measuring durations may be less meaningful as even short durations of agonistic interaction can have a big and lasting impact on welfare.

Agonistic interactions 1: involving** Varecia **species

More of the agonism initiated by *L. catta* was directed at *V. rubra* than any other species, despite *L. catta* only being housed with them in three of the 10 exhibits; 93% of this aggression was observed in one exhibit (directed towards two elderly individuals housed in Exhibit 2). Although inter-specific agonism was rarely recorded at Exhibit 7, the pair of elderly *V. rubra* housed in this exhibit were prevented from leaving their indoor exhibit by the *L. catta* group. When agonistic interactions occurred, they were either associated with *L. catta* chasing the *V. rubra* back into their indoor exhibit or away from the feeding area. The *V. rubra* rarely left their indoor exhibit; therefore, the low frequency of inter-specific agonistic interactions recorded at this location should not be interpreted as evidence of a harmonious relationship between the two species. The welfare of *Varecia* species in these groups was almost certainly compromised by this harassment. Whilst no injuries or abnormal behaviour had been recorded by keepers, such limitations on movement are likely to reduce behavioural diversity and may impact on other aspects of physical health and mental well-being. Ziegler (2002) also documented intense aggression between *L. catta* and *V. rubra*, leading to injury of an *L. catta* individual and permanent separation of the species. The zoo in question was notified.

In the two exhibits housing *V. variegata*; they were most frequently the aggressors towards *L. catta*. They showed the most aggression towards *L. catta* compared to any other lemur species, except for the *E. macaco* housed in Exhibit 9 and *E. rufus* in Exhibit 2 (see 'agonistic interactions 2'). Others have noted *V. variegata* directing aggression towards *L. catta* in polyspecific exhibits (Gecewicz 2001; Manna et al. 2007). Baden et al. (2016) considered the levels of male directed aggression from females within troops of *Varecia* species as 'high'. The *L. catta* groups housed in Exhibits 6, 5 and 1 contained only males. It is possible that females in the *Varecia* groups may have been responsible for many of the agonistic interactions directed towards the male *L. catta* in these exhibits.

Agonistic interactions 2: involving Eulemur macaco

In Exhibit 9, a pair of *E. macaco* acted as the aggressors in 81% of agonistic interactions with *L. catta*. This is much higher than in Exhibit 6 (the only other zoo included in this study which housed the

species), where 8% of agonistic interactions were directed towards *L. catta*. Seventy one percent of the interactions recorded in Exhibit 9 occurred during food presentation. A survey of European zoos housing *L. catta* described the removal of *E. macaco* from their exhibit due to unacceptable high levels of aggression directed towards *L. catta* (Law 2018). There is no research, from wild or captive studies, which suggests this species is more agonistic than others. Conversely, the second highest frequency of inter-specific affiliative behaviour (predominantly proximity) was also recorded in this exhibit. *E. macaco* have the same social structure as *L. catta* (multi-male, multi-female) and display female dominance (Bayart and Simment 2005; Marechal et al. 2010). It is possible that the female *E. macaco* in is this exhibit was responsible for much of the aggression recorded, directing it towards the males in the bachelor *L. catta* group; this could explain why the pair of *E. macaco* in this exhibit were the aggressors much more frequently when compared to the *E. macaco* pair in Exhibit 6 where females of other lemur species were present. These findings may suggest that housing this combination of species when no female *L. catta* are present may require greater monitoring and management intervention from keepers in specific situations, for example, during feeding. Unfortunately, identifying specific individuals was not possible in this study, therefore specific conclusions regarding this hypothesis cannot be made.

Agonistic interactions 3: involving other Eulemur species

Outside the pairings mentioned above, little evidence was found for aggression between other combinations of co-housed lemurs: no agonistic interactions were recorded between *E. albifrons* and *L. catta*, and only one occurrence of *L. catta* displacing *E. mongoz* was observed. Only one agonistic event was recorded between *L. catta* and *E. collaris*, where the individual of the latter species acted as the aggressor. Ziegler (2002) described successful housing of *L. catta* and *E. albifrons* in a German zoo, managed through wide dispersal of food. Taylor (2009) also noted no reports of intense aggression between the species at Taronga Western Plains Zoo. Ellwanger (2002) concluded that inter-specific aggression between *L. catta* and *E. collaris* did not increase during times of food scarcity in wild groups; both species used the same area of canopy at the same time and the author described the relationship as 'harmonious'. Interactions between *E. mongoz* and *L. catta* in either wild or captive contexts, have not been published, therefore comparisons cannot be made for these species.

E. mongoz and *E. rubriventer* are the only species within the *Eulemur* genus to display a 'pair-bonded' social structure consisting of a male, a female and offspring (Curtis and Zaramonday 1998; Curtis and Zaramonday 1999; Colquhoun 2011). Both *E. collaris* and *E. albifrons* maintain multi-male, multi-female groups with more relaxed hierarchies (Ossi and Kimlar 2006; Colquhoun 2011; Palagi and Norscia, 2015). It is possible that where more flexible and potentially weaker hierarchies exist in species housed with *L. catta*, less competition occurs, resulting in fewer inter-specific agonistic events. Further investigation of interactions between these species when housed together is needed to confirm such a hypothesis; however, these finding may provide early indications that *E. mongoz*, *E. collaris* and *E. albifrons* are particularly suitable for housing with *L. catta* in captivity.

Affiliative interactions

Only one affiliative interaction involving physical contact was recorded (during 100 hours of observation), occurring between *L. catta* and either of the *Varecia* species housed with them (see Table 6). This behaviour was most frequently observed with *E. rufus* and *E. macaco* (see Figure 5). For these species, higher proportions of allogrooming, huddling, nose touching, and play were associated with only two specific exhibits (out of 6) co-housing these species. Inter-specific play was predominately observed in Exhibit 2 and was mostly associated with play between and with infants. Most of the affiliative behaviour observed between *L. catta* and *E. macaco* occurred in Exhibit 9, with far less interaction observed in Exhibit 6 where the exhibit was much larger, contained more tall trees and provided separate housing for each species located in different positions around the exhibit. In Exhibit 9 both species shared one indoor space and the area just outside of the exhibit was facing south-west where both species would thermoregulate (huddle and sunbathe); these shared limited resources were most likely the cause of higher proportions of affiliative behaviours in this exhibit.

Larger exhibits significantly predicted decreases in the duration of inter-specific affiliative interactions (see Table 4) and may be associated with more widely distributed resources. Higher levels of proximity in smaller exhibits may have been caused by restrictions on space and/or by bunching of preferred resources, which forced lemurs to spend more time closer together.

Study limitations

Provisioned feeding events rarely lasted more than 30 min but observations in the 'food' condition occurred for two hours. The shared use of these feeding sites appeared to last only as long as the food resources were available. The 'food' observations may have been too long and therefore included data which should have been included in the 'low competition' category. This may have 'diluted' the data for frequency and duration of inter-specific interactions during the 'Food' condition, masking potentially significant impacts of feeding on aggression.

Implications for captive care

Inter-specific agonistic interactions were only slightly more frequent than inter-specific affiliative interactions overall, and both were less frequent than intra-specific interactions observed in captive *L. catta* (Saucier 2008; Shire 2012; Spiezio et al. 2017;) (Hypothesis 1). The presentation of food did not influence inter-specific interactions between *L. catta* and other lemur species in polyspecific exhibits (Hypothesis 2), and the genera housed with *L. catta* did not predict frequency or duration of inter-specific interactions of any type (Hypothesis 3). Total inter-specific agonism was slightly higher between *L. catta* and *Varecia* species, compared with *Eulemur* species, however not significantly so. Total inter-specific affiliative interactions were more frequent between *L. catta* and *Eulemur* species, when compared to *Varecia* species, but not significantly so. Proximity was the most common type of inter-specific affiliation and was most likely linked to species sharing space when utilising resources such as food, climbing opportunities or prime spots for thermoregulation.

When designing polyspecific exhibits for lemurs, consideration must be given to entrances and exits to indoor spaces. Where species are forced to pass each other, harassment and restriction of movement of one or more species may occur. Provision of 'safe' spaces, which restrict access for certain species has proved successful when housing other primates polyspecifically (see Buchanan-Smith et al. 2013). This approach, however, often relies on strategically sized openings/passageways, which due to the similarity in body size of all the lemurs observed in this study, may prove difficult to implement.

L. catta were most frequently the aggressors during agonistic inter-specific interactions and, in two exhibits, directed higher levels of aggression towards pairs of elderly *V. rubra*. Overall, however, agonistic inter-specific interactions were rare. Housing these *L. catta* with other lemurs did not cause higher levels of agonism than they would otherwise experience when housed in a single-species exhibit. This suggests that at group level, these *L. catta* were not experiencing poor welfare (Dixon 1993; Barret et

al. 2002; Honess and Marin 2006). Polyspecific housing with the lemur species included in this study was, therefore, considered suitable for *L. catta*. Co-housing situations with small groups of elderly individuals (particularly of *Varecia* species) should be monitored closely, however, as such individuals may experience poorer welfare resulting from continued harassment. Further, individual-level welfare assessment of both *L. catta* and *Varecia* species (particularly older individuals) is required to ascertain the suitability of housing these specific groups together and determine the welfare status of individual animals.

Higher frequencies of inter-specific affiliative interactions between *L. catta* and *E. rufus* may indicate welfare benefits; however, further individual-level welfare assessment of both species when housed together is required to confirm this. The extremely rare aggression observed between *L. catta* and *E. mongoz*, *E. collaris* and *E. albifrons* may indicate that these species are more suitable for housing with *L. catta* in captivity and that the effect on welfare of all species was at least neutral.

Considerations for future studies of polyspecific exhibits housing lemurs

Only one zoo included in this study housed *L. catta* with *Varecia* species only (EX7). Inter-specific agonistic and affiliative behaviour were significantly lower at this zoo, primarily because the *V. rubra* rarely left their indoor exhibit as, when they did, they were usually harassed through non-contact aggression, back to their indoor quarters. Future investigations need to include more exhibits where *L. catta* are only housed with *Varecia* species to have a more reliable understanding of how these species interact and establish whether housing *L. catta* and one species from the *Varecia* genus is appropriate for the welfare of either species. This also emphasises the need for individual-level welfare assessment.

The characteristics of Exhibit 2 were considerably different to the others included in the study. It was one of only two zoos to house three lemur species with *L. catta*. It was the only exhibit included in the study where *L. catta* were not the biggest troop housed, and in this exhibit, *L. catta*, *E. rufus* and *E. rubriventer* had juvenile individuals aged less than two years of age. Future investigations should incorporate more exhibits with these characteristice to better understand their impact on interactions.

This investigation focussed on the compatibility of *L. catta* with other lemur species when housed polyspecifically, therefore only interactions between *L. catta* and other lemur species were recorded. In exhibits where three or more species were housed, interactions between the other lemur species may have provided greater insight regarding suitable combinations for housing. Where for example, higher frequencies of inter-specific agonistic interactions were recorded between *L. catta* and *Varecia* species, information relating to the frequency of agonism between *Varecia* and other lemurs could have established whether *Varecia* species were generally more agonistic towards all lemur species when housed polyspecifically, or just *L. catta*. Future research in this area should focus on inter-specific interactions between these other species groups to provide a more thorough understanding of the impacts of mixed-species housing on all the species affected.

This paper has investigated inter-specific interactions involving Lemur catta housed in mixed-species exhibits in UK zoos. Although its findings are invaluable in understanding these issues, the authors acknowledge that 'local' factors (health status, history, management, husbandry, enclosure design, hierarchies, etc.) play an important role in influencing the behaviour of captive lemurs. As a result, the importance of monitoring cannot be underestimated.

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