

Inter-species encounters among diurnal primates in Danum Valley, Borneo

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**Abstract** Polyspecific associations, in which individuals of multiple species move together, have not been reported in Asian primates. However, only one study in India has shown this lack of association quantitatively. We collected data on inter-species encounters among five species of diurnal primates in Danum Valley by censusing four predetermined routes of 9.9 km, covering 1544.3 km, and tracking red leaf monkeys (*Presbytis rubicunda*) for 423 h over 25 months. We tested the null hypothesis that the frequency and duration of encounters did not differ from chance levels. During censuses, we detected primates 373 times, and found two species on the same 100-m segment only six times. This frequency was not significantly different from the chance level. While following red leaf monkeys, the frequency of encounters was lower than expected by chance with Müller's gibbons (*Hylobates muelleri*) but higher than expected by chance with Bornean orangutans (*Pongo pygmaeus*) in the non-fruiting season. Inter-species encounters accounted for 6.4% of tracking time, and the encounter duration was significantly longer than expected by chance for orangutans. Red leaf monkeys did not change their rate or direction of travel upon meeting another species. We could not distinguish the association between red leaf monkeys and orangutans in the non-fruiting season from the possibility that the two species were independently attracted to the same place. In conclusion, we show the absence of active and consistent polyspecific association and identify avoidance in some species-pairs in an Asian primate community.

Key words: community ecology; gas model; inter-species relationships;  
polyspecific association; ranging

## Introduction

Many primates live sympatrically with other species of primates. Relationships among sympatric primates are diverse, including predation, competition, commensalism and mutualism (Reed & Bidner, 2004), and the interactions observed during inter-species encounter also vary. There are reports of both agonistic interactions, such as threat (Houle et al., 2006) or even hunting (Uehara, 1997) and affiliative interactions, such as grooming (Eppley et al., 2015; Ihobe, 1997). One notable inter-species interaction is polyspecific association, in which groups of multiple species move together for a few hours or even almost permanently (Heymann & Buchanan-Smith, 2000). The two main hypothesized advantages of polyspecific associations are predation avoidance and increased feeding efficiency (Bryer et al., 2013; Chapman & Chapman, 1996). Living in a larger group can reduce the risk of predation by dilution, as well as increased detection and counter-attack abilities (van Schaik, 1983). When the costs of increasing group size greatly outweigh the benefits of doing so, formation of a polyspecific association is one option to make group size larger, without some of the associated costs (Oliveira et al., 2017). Some primates can benefit by ranging with another species which is better at detecting predators (Buzzard, 2010; McGraw & Bshary, 2002) or open hard foods that they cannot open themselves (Pineiro et al., 2011).

Groups of different species may encounter each other by chance even if they move randomly, so a high frequency and duration of inter-species

encounters do not necessarily indicate active formation of a polyspecific association. One way to test this is to compare observed and expected values of the frequency and duration of inter-species encounters. We can derive expected values from a model in which primate groups move randomly like gas molecules and calculate the expected values using group density, velocity of movement, and spread (Hutchinson & Waser, 2007; Waser, 1982). However, unlike gas molecules, primate groups do not move randomly, so this model (Hutchinson & Waser, 2007; Waser, 1982) does not distinguish active formation of polyspecific associations from the independent aggregation of multiple species at a specific place (e.g., a food patch). Despite this limitation, the gas model is commonly used to identify active formation of a polyspecific association (Holenweg et al., 1996; Shaffer et al., 2016). An alternative approach is to conduct a census over a large area and use the results to determine whether any species-pairs are detected simultaneously more often than expected by chance (Astaras et al., 2011; Haugaasen & Peres, 2009). This method is useful when studying a primate community as a whole or a species which occurs at low density or is difficult to track. It may also be possible to show active polyspecific association by showing coordination of movement patterns by two groups of different primate species (Heymann, 2011), although there are few examples of this (Go, 2010).

Most studies of polyspecific associations are on primates in the Americas and Africa, and there are few reports on this topic for primates in Asia and Madagascar. Some early studies reported the frequency of detection of multiple species at the same place during censuses on the Malay Peninsula and Borneo (Bernstein, 1967; Rodman, 1973, 1978). The frequency was as

high as 18% of detections in one study (Bernstein, 1967), but it is difficult to rule out the possibility that different species occurred together frequently by chance due to the small area of the forest (75 ha) and the large number of groups (17 groups of 5 species) in the study. A study in Western Ghats, India, is the only quantitative examination of polyspecific associations in Asia using the Waser gas model (Erinjery et al., 2016). The frequency and duration of encounters between lion-tailed macaques (*Macaca silenus*) and sympatric bonnet macaques (*M. radiate*) or Nilgiri langurs (*Semnopithecus johnii*) did not differ from or were lower than those expected by chance. Single individuals join groups of different species in two species of langurs (purple-faced langur *Semnopithecus vetulus* and tufted gray langur *S. priam*) in Sri Lanka (Lu et al., 2021), but this behavior is different from the association of groups of different species reported in African and American primate communities. We need more studies of inter-species encounters to understand the lack of polyspecific associations in Asia, in particular for a species-rich primate community with a different set of species from that investigated in India.

We aimed to examine whether five species of diurnal primates in Borneo encounter each other more or less often than by chance. We focused on Bornean orangutans (*Pongo pygmaeus*), Müller's gibbons (*Hylobates muelleri*), red leaf monkeys (*Presbytis rubicunda*), long-tailed macaques (*Macaca fascicularis*), and southern pig-tailed macaques (*M. nemestrina*). First, we censused primates and determined whether the frequency of detecting multiple species at the same place differed from that expected based on their abundance. Second, we compared the observed frequency and duration of inter-species encounters while tracking a group of red leaf monkeys with

expected values calculated by the gas model (Hutchinson & Waser, 2007).  
 Third, we analyzed the red leaf monkeys' movement before and during the  
 encounter to find whether the group actively avoided other species. If the group  
 intended to avoid a place occupied by another species, we predicted they would  
 change their direction of movement (angle) or increase their travel rate to leave  
 the encounter quickly.

## Methods

### *Study site*

The study site was a primary lowland dipterocarp forest around Danum Valley  
 Field Centre (4°57'N, 117°48'E, 300 m above sea level) in Danum Valley  
 Conservation Area (438 km<sup>2</sup>) in eastern Sabah, northern Borneo (Fig. 1; Hanya  
 and Bernard (2012, 2013)).

### *Primate census*

We set four census routes of 9.9 km, using existing trails that mostly run straight  
 in a north-south or west-east direction. We divided each route into 99 segments  
 of 100 m in length. We conducted the census 2-10 times/month from December  
 2006 until December 2008 (mean: 5.5 times/month), with a total distance of  
 1544.3 km. Two observers (our field assistants) walked together, slowly, looking  
 upward, at approximately 1 km/h. The census started around sunrise (06:00-  
 06:15h) and ended around 11:00h. When they detected a primate, including  
 single animals, the observers recorded the species, segment ID, and the  
 distance between the center of the group and the nearest point of the trail to the  
 group. We observed a group for a maximum of 10 min, but in most cases the

primates fled immediately after detection. The data are the same as those used in Hanya et al. (2020).

To estimate the population density of orangutans, we conducted a nest census of orangutans once a month along the same census routes and during the same period as the route census. We used the marked nest census technique, which counts only nests made since the previous census (Kanamori et al., 2017). After a trial period of a few months, two observers walked the census trail looking upward, and when they detected an unmarked orangutan nest, they recorded the location and marked it.

#### *Direct tracking of primate groups*

We tracked and conducted direct observations on the five species of primates from December 2006 through December 2008. Our main study aim concerned the feeding ecology of red leaf monkeys, and we followed other species only when we had enough data for red leaf monkeys in that month or when we could organize two tracking teams. Our total observation time was 1141 h for red leaf monkeys (158 days over 25 months), 127 h for orangutans (16 days over 10 months), 72 h for gibbons (32 days over 14 months), 22 h for pig-tailed macaques (15 days over 8 months), and 13 h for long-tailed macaques (5 days over 5 months). Every 10 minutes, we recorded the location of the group by GPS (GPSmap 60CSx). When GH was in the tracking team, we also recorded the presence/absence of other species while following a focal group of any species. We recorded whether that species was still visible at the next 10 minute sample. GH was in the team and recorded presence/absence of other species for 423 h for red leaf monkeys, 36 h for orangutans, 27 h for gibbons,



10 h for pig-tailed macaques, and 4 h for long-tailed macaques. Although we tried to follow primates for as long as possible, tracking was possible only within the home range (21 ha) of the focal group of habituated red leaf monkeys (Hanya & Bernard, 2016) because we were not familiar with the terrain outside of it.

### *Data analysis*

We estimated the group density of gibbons, red leaf monkeys, long-tailed macaques, and pig-tailed macaques using Distance 5.5 (Buckland et al., 1993). We excluded solitary animals from the estimation. We selected among models with different combinations of detectability function and adjustment terms based on AIC. We used nest census to estimate the density of orangutans, following the method of Kanamori et al. (2017). The density of orangutans estimated using the route census, which was based on a much smaller number of detections (N=53) than the nest census (N=345), was implausibly higher (20.9 ind/km<sup>2</sup>) than the previous estimate in Danum Valley (1.3; Kanamori et al. (2017)).

Based on the total number of segments walked (N=15,443), and the numbers of detections of species 1  $d_1$  and species 2  $d_2$ , we calculated the probability that we would detect these two species in the same segment zero ( $P_0$ ), one ( $P_1$ ), two ( $P_2$ ), and three times ( $P_3$ ) under the null hypothesis that the two species were in the same segment only by chance (Supporting Information S1) as

$$P_0 = \prod_{j=0}^{d_1-1} \frac{N-d_2-j}{N-j} \quad (1),$$

$$P_1 = d_1 * \frac{d_2}{N} * \prod_{j=1}^{d_1-1} \frac{(N-j)-(d_2-1)}{N-j} \quad (2),$$

$$P_2 = \frac{d_1(d_1-1)}{2} * \frac{d_2}{N} * \frac{d_2-1}{N-1} * \prod_{j=2}^{d_1-2} \frac{(N-j)-(d_2-2)}{N-j} \quad (3), \text{ and}$$

$$P_3 = \frac{d_1(d_1-1)(d_1-2)}{6} * \frac{d_2}{N} * \frac{d_2-1}{N-1} * \frac{d_2-2}{N-2} * \prod_{j=3}^{d_1-3} \frac{(N-j)-(d_2-3)}{N-j} \quad (4).$$

We calculated  $P_{>3}$  as  $1-P_0-P_1-P_2-P_3$ . When the two species were on the same segment once, for example, we rejected the null hypothesis if  $P_1+P_2+P_3+P_{>3}$  was below 0.005. We used a Bonferroni correction to determine statistical significance: the adjusted alpha was 0.005 because there were 10 species-pairs.

The gas model predicts the expected frequency of inter-species encounters during tracking of the red leaf monkey group as  $2\rho D(\sqrt{\bar{u}^2 + \bar{v}^2})$ , and expected duration as  $\frac{\pi * D}{2\sqrt{\bar{u}^2 + \bar{v}^2}}$ , where  $\rho$  is the group density of other primate groups (or individuals, in the case of orangutans),  $D$  is (group spread of red leaf monkey+group spread of other species+detection distance)/2,  $\bar{u}$  is the mean travel rate of red leaf monkeys, and  $\bar{v}$  is the mean travel rate of other species (Hutchinson & Waser, 2007). We calculated the mean travel rate from our location data for the five species and estimated group spread visually during tracking (Table 1). The distance between two encountering groups was 50 m at maximum; however, we were not sure if we recorded all of the cases in which inter-group distance was less than 50 m. Therefore, we also calculated the expected values when detection distance was 30 m, a distance at which we were unlikely to overlook the presence of any second species. Under the null hypothesis, the probability of  $\leq i$  encounters is  $\sum_{j=0}^i \frac{\mu^j e^{-\mu}}{j!}$ , and the probability of  $\geq i$  encounters is  $1 - \sum_{j=0}^{i-1} \frac{\mu^j e^{-\mu}}{j!}$ , where  $\mu$  is the predicted number of encounters (Hutchinson & Waser, 2007). Based on this probability, we examined whether the observed number of encounters was different from the chance level using two one-tailed tests. For example, if the number of observed encounters was

three, we examined whether the probabilities of  $\geq 3$  and  $\leq 3$  encounters were lower than alpha, which we set at 0.025 ( $=0.05/2$ ; Bonferroni correction) in this test.

Only orangutans exhibit seasonal fluctuations in abundance in Danum Valley (Hanya et al., 2020). During the study, a fruiting event drove an increase in abundance (Kanamori et al., 2017). Therefore, we analyzed data for fruiting (May-October 2007) and non-fruiting seasons (other months, Hanya et al. (2020)) separately for orangutans. We tested the difference between the expected and observed duration of encounters using a Wilcoxon rank sum test (Erinjeri et al., 2016) using the function *wilcox.exact* in the package *exactRankTests* of R 3.6.1 (R\_Core\_Team, 2019). To test the encounter duration, we also included three cases in which the focal group was another species (N=2 for gibbons and N=1 for pig-tailed macaques) and that group encountered red leaf monkeys. Density does not affect the estimation of expected encounter duration, so we did not separate the data by season for our analysis of encounter duration.

Our data on travel rate were for a limited area (21 ha) and based on short-term tracking records for species other than red leaf monkeys. For comparison, we also calculated expected values using travel rates reported in similar habitats (lowland dipterocarp forest; Table 1). For gibbons, we divided the reported value of daily path length of two groups in Danum Valley (Inoue et al., 2016) by 8 h, since these gibbon groups become inactive on average four hours before sunset and there are 12 h of daylight. For orangutans, we used unpublished data collected by Tomoko Kanamori, who conducted full-day follows of orangutans for 22 days in Danum Valley, dividing the daily path length

by 12 h. For long-tailed macaques, we divided the reported daily path length reported for Kutai, Borneo (Wheatley et al., 1996) by 12 h. For pig-tailed macaques, we used the travel rate reported in Pasoh, Malay Peninsula (Caldecott, 1986).

We tested whether there was any change in the distance travelled in 10 min or the angle ( $0-\pi$ ) of movement before and during an encounter between the red leaf monkey group and a different species. We converted the location data of the red leaf monkey group into trajectory using the function *as.ltraj* of the package *adehabitatLT* in R. We discarded data when the automatic recording of the GPS failed and we did not have data for the 10 min interval. We did not use angle data for the first record of that day or if the group had moved  $< 20$  m in the previous 10 min because we could assess the change in the direction of movement. For a trajectory of  $< 20$  m, indicating the group stayed within the location error of the GPS, we set the angle as 0 and concluded that the group did not change its movement pattern in the sense that it stayed at almost the same place. We used a two-tailed Wilcoxon signed rank test to compare the trajectory during the inter-species encounter and the previous trajectory using the function *wilcox.test* in R with an alpha level of 0.05. We ran analyses for all species combined and for each species separately.

#### **Data availability**

The datasets generated and/or analysed during the current study are not publicly available but are available from the corresponding author on reasonable request.

## **Ethical note**

The research complied with the “Guidelines for field research on non-human primates” of the Primate Research Institute, Kyoto University. The research also adhered to the legal requirements of Malaysia and Japan.

## **Results**

### *Detection of two species on the same segment during a route census*

We detected some pairs of species on the same segment of the census route, but the frequency was only at chance level. Two species were on the same segment in 3.2% of observations (6 instances \* 2 species / 373 total instances). The probability of detecting both species on the same segment for the observed number of times under the null hypothesis was above the alpha level for all species-pairs (Table 2).

### *Inter-species encounters while tracking red leaf monkeys*

In total, we observed 37 inter-species encounters while tracking red leaf monkeys (Supporting Information S2). We observed no encounters with solitary animals except for orangutans. Ten encounters included agonistic interactions, such as overt aggression, threat, or one species supplanting another. Orangutans and pig-tailed macaques supplanted other species multiple times. While we were tracking the red leaf monkey group, the frequency of encounters with gibbons was lower than expected by chance (Table 3). The frequency of encounter with orangutans varied with season and was higher than expected by chance in the non-fruiting season, but not in the fruiting season (Table 3). When we used data from previous studies, the encounter frequency with long-tailed

macaques was lower than expected by chance, but the results for the other species were the same as when we used our own data (Table 4). Encounters with orangutans were longer than expected by chance (Table 5). Results for encounter duration did not change when we used travel rate data from previous studies (Table 6). The total duration of encounters was 6.4% of red leaf monkey tracking time. Neither the frequency and duration of encounters with pig-tailed macaques were significantly different from the chance level (Tables 3, 4, 5 and 6).

#### *Changes in red leaf monkey ranging when they encountered other species*

The red leaf monkeys did not change their speed or angle of travel when they encountered another species. They showed no change in either the distance travelled (Wilcoxon signed rank test:  $N=28$ ,  $W=414$ ,  $P=0.906$ ) or angle of movement ( $N=27$ ,  $W=404$ ,  $P=0.804$ ) before and during an encounter. We also found no difference when we analyzed the species encountered separately for both length (gibbon:  $N=8$ ,  $W=26$ ,  $P=0.902$ ; orangutan:  $N=9$ ,  $W=47$ ,  $P=0.605$ ; long-tailed macaque:  $N=9$ ,  $W=46$ ,  $P=0.667$ ; pig-tailed macaque:  $N=2$ ,  $W=1$ ,  $P=0.400$ ; Fig. 2) and angle (gibbon:  $N=7$ ,  $W=36$ ,  $P=0.382$ ; orangutan:  $N=9$ ,  $W=27$ ,  $P=0.208$ ; long-tailed macaque:  $N=9$ ,  $W=38.5$ ,  $P=0.856$ ; pig-tailed macaque:  $N=2$ ,  $W=4$ ,  $P=0.683$ ; Fig. 3).

## **Discussion**

### *Lack of active and consistent formation of polyspecific associations*

Diurnal primates in Danum Valley did not seem to form polyspecific associations actively and consistently. During the census, we did not detect any two species

on the same segment more often than by chance. When we were tracking a group of red leaf monkeys, they encountered other species only at a chance level, with the exception of orangutans, which they encountered more often than expected by chance in non-fruiting months. The red leaf monkey group was with other species for 6.4% of the observation time. Direct comparison is difficult due to methodological differences, but this figure is much smaller than the association rates reported for African and American primate groups (Table 7). In Africa, the percentage of time spent associating with all other sympatric primates is 17-100%. Small primates in Central and South America, such as tamarins (*Saguinus* spp), squirrel monkeys (*Saimiri* spp), and lion tamarins (*Leontopithecus* spp), associate with other primates 10-82% of the time. According to community-level censuses, 6-47% of detections involved multiple species at six sites in Kibale, Uganda (Chapman & Chapman, 2000), 44% in Korup, Cameroon (Astaras et al., 2011), and 10% in Lago Uauaçu, Brazil (Haugaasen & Peres, 2009), all of which are higher than the frequency observed in this study (1.6% if we regard the detections of two species on the same segment as a single detection).

Encounters between red leaf monkeys and orangutans were more frequent in non-fruiting months, and were longer than expected by chance. Due to the limitations of the gas model, we cannot conclude whether this was due to active formation of polyspecific associations or to the independent aggregation of the two species to a particular place, such as a food patch. Red leaf monkeys did not change their travel pattern before and during an encounter with orangutans, which suggests that encounters are passive events for red leaf monkeys. The fact that the two species encounter one another more frequently

than by chance in the non-fruiting season but not in the fruiting season, also supports the hypothesis that the two species were independently attracted to a limited number of fruiting trees. In six of 10 encounters in non-fruiting months, we observed the primates eating fruit or seeds during or within 20 min of the encounter. We need ranging data for orangutans to determine whether they seek out red leaf monkeys. In any case, the encounters were infrequent (every 32.5 h or once every 2.7 days) and short (0 h 20 m-1 h 43 m), so this association may have little impact on the survival of the red leaf monkeys in terms of predation avoidance or increased foraging efficiency. One reason why we found this pattern only for orangutans, and not for other species, may be that their travel rate is similar to that of red leaf monkeys (Table 1). Dietary overlap may also affect association patterns (Pineiro et al., 2011; Sushma & Singh, 2006). Diet at least partially overlaps between red leaf monkeys (Hanya & Bernard, 2012) and orangutans (Kanamori et al., 2010), but it is not yet clear whether this degree of overlap is larger than that for other species-pairs in this primate community. Simultaneous tracking of the two species would help to understand how these two species encounter one another and maintain proximity.

#### *Inter-species agonism and avoidance of other species*

We observed, though infrequently, inter-species aggressive interactions or one species supplanting another species from a tree in six out of 10 species-pairs. Orangutans and pig-tailed macaques were dominant over other species, which could be related to their larger body mass (All the World Primates database: <https://www.alltheworldsprimates.org/>) and the larger group size of pig-tailed



macaques (53 in a forest-oil palm plantation mosaic of Segari Melintang, Malay  
Peninsula (Ruppert et al., 2018); 25-35 in Pasoh (Caldecott, 1986)) than the  
 other species we studied. These two species may dominate other species in  
 inter-species feeding competition, but the effect on food acquisition may not be  
 large considering the low frequency of such interactions.

We found a lower frequency of encounter of red leaf monkeys with  
gibbons than expected by chance. This pattern remained unchanged if we  
adopted a different definition of detection distance. We also found a lower  
encounter frequency between red leaf monkeys and long-tailed macaques than  
expected by chance when we used data from previous studies, but not those  
from our own study. In spite of the lower-than-expected frequency of inter-  
species encounter, our analysis of the movement of the red leaf monkeys did  
not show that they avoid other species (Fig. 2). If they tried to leave a place  
where they encountered another species, we predicted that they would move  
quickly or change their direction of movement, but we did not find this. Once red  
leaf monkeys are close to a group of another species, they do not seem to  
respond conspicuously, although they may alter their ranging if they can detect  
the presence of other species from several hundred meters away, for example  
by hearing gibbons' loud calls (songs) (Clink et al., 2020). The frequency of  
 agonistic interactions with other species was low, and there is no fatal risk such  
 as predation. The advantage of active avoidance may not be large enough to  
 cover the cost of a sudden and major change of movement.

#### *Parameters used in the gas model*

In addition to travel rate estimates, our results also rely on other parameters

used in the gas model, such as group density. Our census was not an ordinary line transect because 39% of the route was not straight. However, this does not pose a serious problem in the estimation of group density as long as the route covers various environments randomly (Buckland et al., 1993). The non-straight part included ridges, slopes and valleys. Calculated group densities of red leaf monkeys ( $7.65/\text{km}^2$ ) and gibbons ( $4.67/\text{km}^2$ ) were in accord with their home range sizes in this area (21 ha for red leaf monkeys and 33 ha for gibbons; Hanya and Bernard (2016), Inoue et al. (2016)), assuming some degree of overlap among groups. The calculated population density of orangutans ( $2.1\text{ ind}/\text{km}^2$ ) was not very different from the estimate based on a much larger dataset from another study site in Danum Valley ( $1.3\text{ ind}/\text{km}^2$ ) (Kanamori et al., 2017).

We tracked all of these species in both fruiting (May-October 2007) and non-fruiting months (Hanya & Bernard, 2012), so it is unlikely that the estimation of travel rate is biased seasonally. Although the results on avoidance between red leaf monkeys and long-tailed macaques differed with the source of travel rate data, our conclusion that polyspecific associations are absent in this primate community seems robust.

#### *Implications for polyspecific associations and avoidance of other species among primate communities*

Like the study in India (Erinjery et al., 2016), we found a lack of active and consistent formation of polyspecific association in an Asian primate community. Reviews of primate community ecology suggest a lack of polyspecific association in Asia and Madagascar and link this to the lack of aerial predators

(raptors) (Reed & Bidner, 2004; Terborgh, 1990). However, raptor predation can impose a significant impact on a lemur community (Karpanty, 2006), and polyspecific association is reported in one community in Madagascar, although without a direct test using the Waser gas model (Freed, 2007). The rate at which a pair of lemur species associates is intermediate between Asian and African or American primates (Table 5). Felids are important predators of Asian primates (Bidner, 2014), and Asian primates respond to this risk (Matsuda et al., 2011; Otani et al., 2020). If raptors drive polyspecific association, we need to clarify why polyspecific association is not related to other predators. although without a direct test using the Waser gas model (Reed & Bidner, 2004) and the lack of small species (Ganzhorn, 1999), leads to a lack of polyspecific association. For example, Asian primates may be less vulnerable to predation than African or American primates due to their large body size. Alternatively, due to the small number of species in the community, there may not be any species pairs that travel at a sufficiently similar rate to permit easy coordination of travel movement.

Our analysis suggests that some primate species avoid encounters with other species. This reflects the findings of another study of inter-species encounters in Asia, where lion-tailed macaques avoided Nilgiri langurs (Erinjery et al., 2016). Avoidance has not been the focus of most previous studies on inter-species interaction (Table 5). This may be partly because a statistical test was not possible in the original Waser gas model (Waser, 1982), so it was difficult to distinguish a neutral encounter from avoidance. These behaviors can be distinguished in the updated gas model (Hutchinson & Waser, 2007). The accumulation of data on inter-species encounters, including in communities

426 lacking polyspecific association, will reveal the diversity of inter-species  
427 interactions in primate communities, from avoidance to polyspecific association,  
428 and its ecological drivers.

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629 Figure captions

630 Fig. 1. Location of Danum Valley on the island of Borneo and primate census  
631 routes used in a study of interspecies encounters.

632 Fig. 2. Distance moved (m) during the 10 minutes before and during inter-  
633 species encounters while tracking a group of red leaf monkeys in Danum  
634 Valley, Dec 2006-Dec 2008.

635 Fig. 3. Angle between the travel trajectory and that 10 min previously before and  
636 during inter-species encounters while tracking a group of red leaf monkeys in  
637 Danum Valley, Dec 2006-Dec 2008.

638 Supporting Information S1. Calculation of the probability that two species would  
639 be detected in the same segment.

640 Supporting Information S2. Observed cases of inter-species encounter.

641

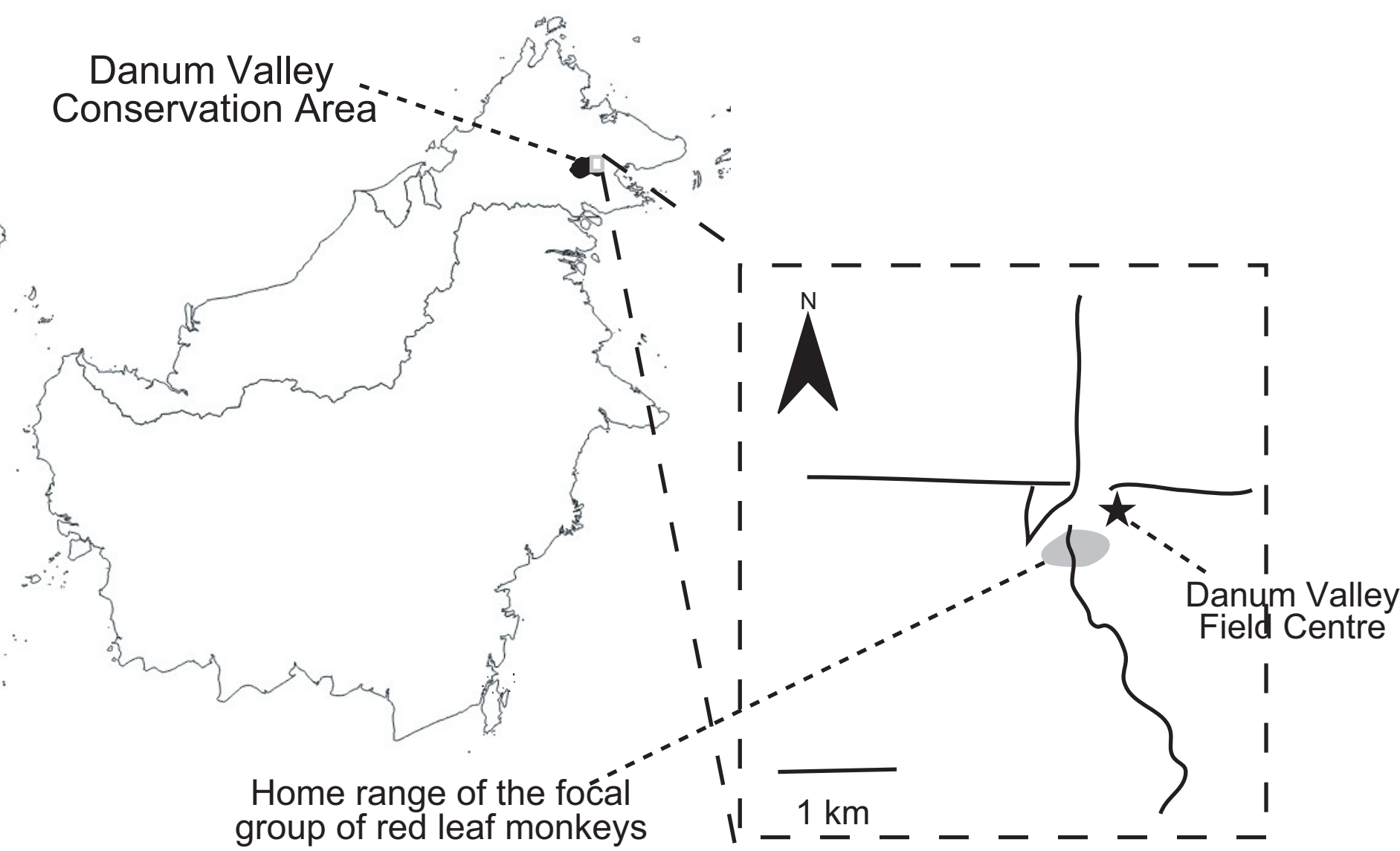
642 (Buchanan-Smith, 1999; Cords, 1990; Gautier-Hion et al., 1983; Heymann,  
643 1990; Oliveira & Dietz, 2011; Pinheiro et al., 2011; Whitesides, 1989)

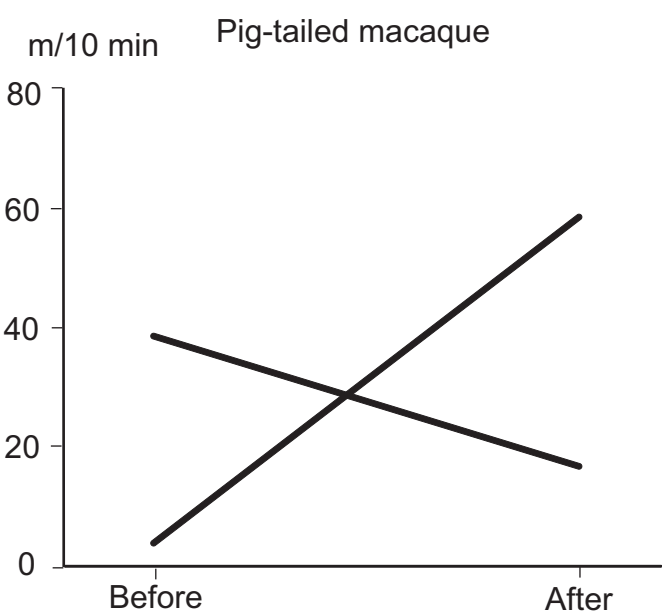
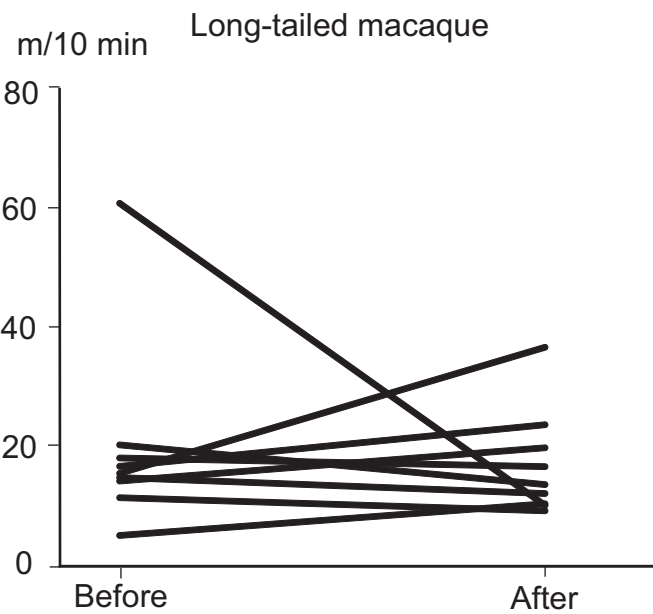
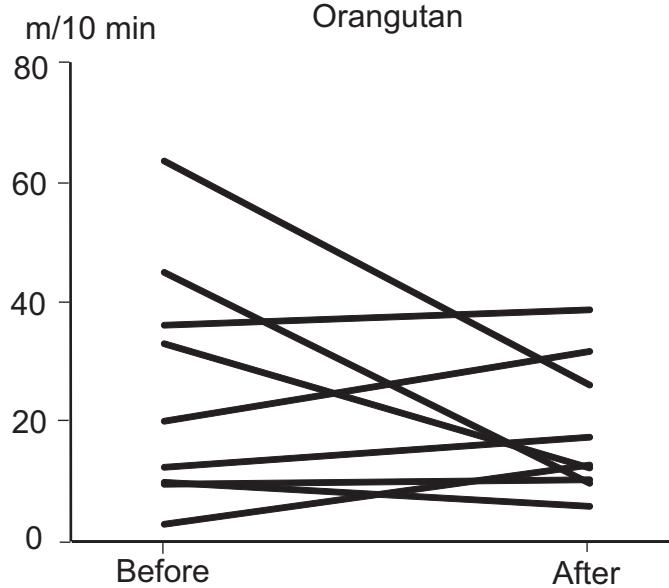
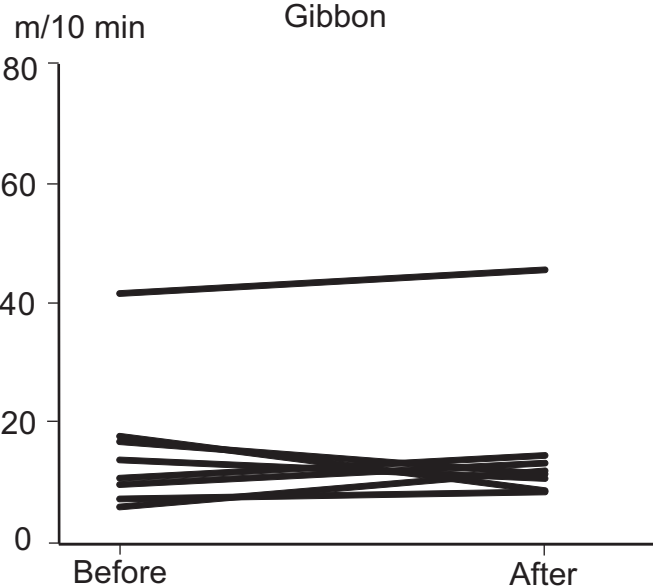
Danum Valley  
Conservation Area

Home range of the focal  
group of red leaf monkeys

1 km

Danum Valley  
Field Centre







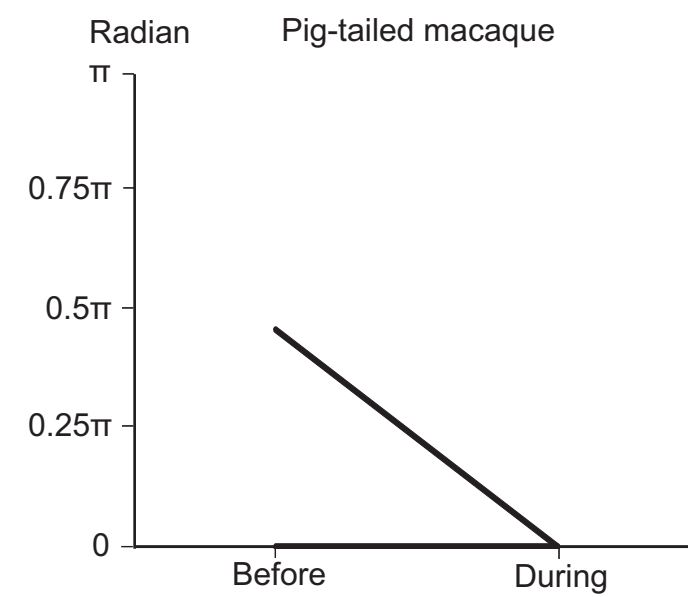
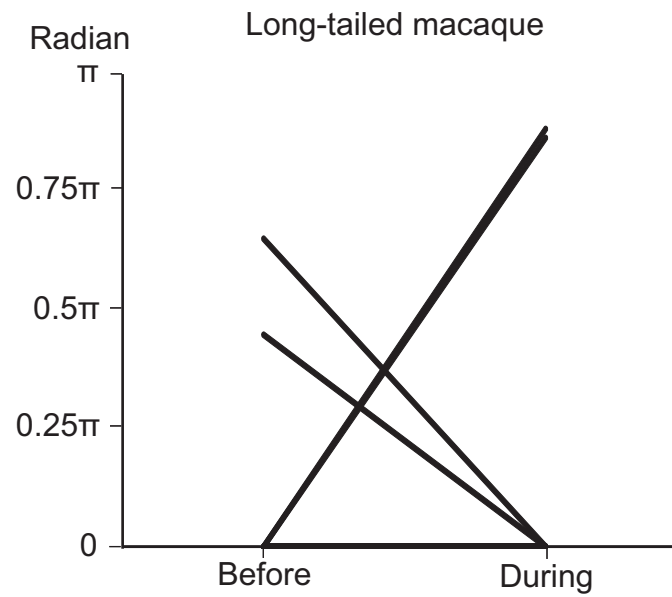
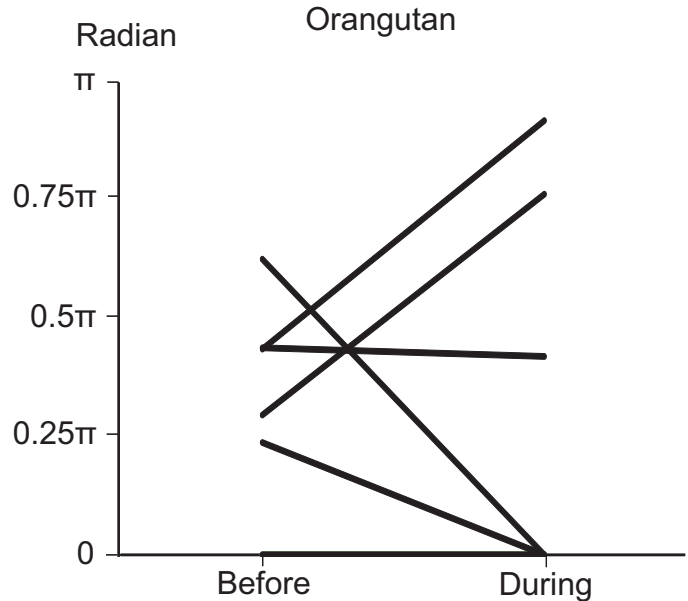
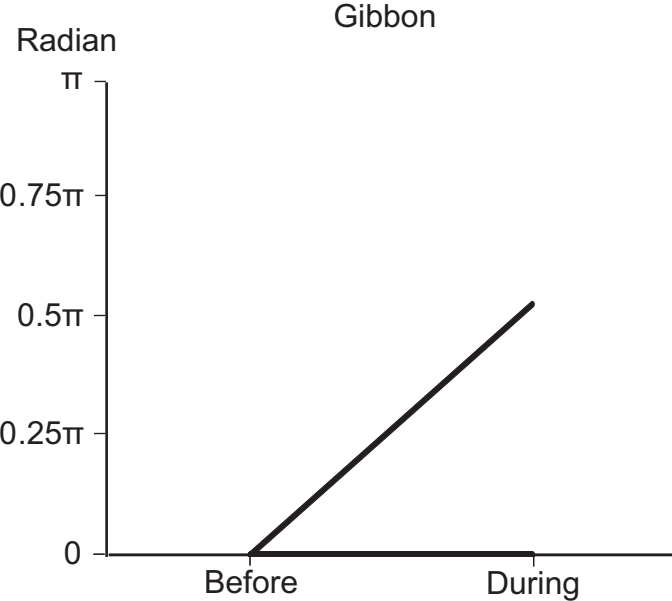


Table 1. Summary of parameters used to calculate the expected frequency and duration of inter-species encounters among diurnal primates in Danum Valley (Dec 2006-Dec 2008)

Parameter	Unit	Gibbon	Red leaf monkey	Orangutan, fruiting season	Orangutan, non-fruiting	Long-tailed macaque	Pig-tailed macaque
Group spread	m	10	20	0		50	50
Group density	/km <sup>2</sup>	4.67	7.65	3.73	1.56	1.08	0.24
Travel rate (this study)	m/h	177	97		96	59	275
Travel rate (previous studies)	m/h	151	97		128	158	312

Table 2. Number of times we detected two species on the same 100 m segment during a census (upper diagonal) and the probability it occurs under the null hypothesis (lower diagonal) among diurnal primates in Danum Valley (Dec 2006-Dec 2008)

	Gibbon	Red leaf monkey	Orangutan	Long- tailed	Pig-tailed macaque
Total number of detection	140	138	53	26	16
Gibbon		3	0	0	0
Red leaf monkey	0.13		0	0	2
Orangutan	0.617	0.621		0	1
Long-tailed macaque	0.789	0.792	0.914		0
Pig-tailed macaque	0.864	0.009	0.054	0.973	

We set the alpha level as  $P=0.005$

Table 3. Observed and expected frequency of inter-species encounters while following a group of red leaf monkeys in Danum Valley (423 h, Dec 2006-Dec 2008) and the probability that the encounter occurs more or less often than the expected number of cases when we calculate the expected frequency using data on travel rate based on our own tracking records

Species	Observed		Expected		Probability observed $\geq$ expected	Probability observed $\leq$ expected
	n	n/h	Detection distance	n/h		
Gibbon	6	0.014	50 m	0.075	1.000	<0.001
			30 m	0.057	1.000	<0.001
Orangutan, fruiting season	3	0.031	50 m	0.036	0.678	0.538
			30 m	0.025	0.455	0.759
Orangutan, non- fruiting season	10	0.031	50 m	0.015	0.027	0.989
			30 m	0.011	0.003	0.999
Long-tailed macaque	13	0.019	50 m	0.015	0.287	0.823
			30 m	0.012	0.154	0.919
Pig-tailed macaque	3	0.007	50 m	0.008	0.689	0.525
			30 m	0.007	0.568	0.656

Table 4. Observed and expected frequency of inter-species encounters while following a group of red leaf monkeys in Danum Valley (423 h, Dec 2006-Dec 2008) and the probability that the encounter occurs more or less often than the expected number of cases when we calculated the expected frequency using data on travel rate based on reported values of previous studies

Species	Observed		Expected		Probability observed $\geq$ expected	Probability observed $\leq$ expected
	n	n/h	Detection distance	n/h		
Gibbon	6	0.014	50 m	0.060	1.000	<0.001
			30 m	0.045	1.000	<0.001
Orangutan, fruting season	3	0.031	50 m	0.042	0.777	0.412
			30 m	0.030	0.562	0.662
Orangutan, non- fruting season	10	0.031	50 m	0.018	0.066	0.968
			30 m	0.013	0.009	0.997
Long-tailed macaque	13	0.019	50 m	0.039	0.993	0.016
			30 m	0.033	0.965	0.067
Pig-tailed macaque	3	0.007	50 m	0.011	0.822	0.349
			30 m	0.009	0.717	0.491

Table 5 Observed and expected duration of inter-species encounters while following a group of red leaf monkeys in Danum Valley (Dec 2006-Dec 2008) with results of Wilcoxon signed rank tests when we calculate the expected frequency using data on travel rate based on our own tracking records

Species	Observed (h)		Detection distance (m)	Expected (h)	V	P
	Mean	SD				
Gibbon	0.98	1.46	50 m	0.31	26	0.297
			30 m	0.23	29	0.141
Orangutan	0.94	0.46	50 m	0.40	87	0.002
			30 m	0.29	89	0.001
Long-tailed macaque	0.89	0.69	50 m	0.83	20	0.820
			30 m	0.69	22	0.625
Pig-tailed macaque	0.67	0.35	50 m	0.32	7	0.625
			30 m	0.27	8	0.375

Table 6 Observed and expected duration of inter-species encounters while following a group of red leaf monkeys in Danum Valley (Dec 2006-Dec 2008) with results of Wilcoxon signed rank tests and the results of the Wilcoxon signed rank test when we calculate the expected frequency using data on travel rate based on reported values of previous studies

Species	Observed (h)		Detection distance (m)	Expected (h)	V	P
	Mean	SD				
Gibbon	0.981	1.459	50 m	0.350	23	0.531
			30 m	0.260	27	0.234
Orangutan	0.940	0.457	50 m	0.340	88	0.001
			30 m	0.240	90	0.001
Long-tailed macaque	0.892	0.689	50 m	0.510	27	0.234
			30 m	0.420	27	0.234
Pig-tailed macaque	0.672	0.351	50 m	0.290	7	0.625
			30 m	0.240	8	0.375

Table 7. Rate of polyspecific association in primate communities estimated by group tracking

Region	Country	Site	Focal species	Species encountered	% asso ciatio	Criterion	Reference
Africa	Uganda	Kibale	<i>Cercopithecus ascanius</i>	All species combined	73	< 50 m	Bryer et al. (2013)*
				<i>Cercopithecus mitis</i>	31		
				<i>Procolobus rufomitratus</i>	30		
				<i>Colobus guereza</i>	23		
				<i>Lophocebus albigena</i>	12		
				<i>Cercopithecus lhoesti</i>	2		
	Uganda	Kibale	<i>Lophocebus albigena</i>	<i>Cercopithecus ascanius</i>	15	< 50 m	Waser (1982)
				<i>Cercopithecus mitis</i>	9		
				<i>Pan troglodytes</i>	1		
	Uganda	Kibale	<i>Cercopithecus mitis</i>	All species combined	17	< 20 m	Cords (1990)
				<i>Cercopithecus ascanius</i>	13		
				<i>Procolobus rufomitratus</i>	7		
				<i>Lophocebus albigena</i>	1		
			<i>Cercopithecus ascanius</i>	All species combined	49		
				<i>Procolobus rufomitratus</i>	31		
				<i>Cercopithecus mitis</i>	28		
				<i>Lophocebus albigena</i>	4		
	Kenya	Kakamega	<i>Cercopithecus mitis</i>	<i>Cercopithecus ascanius</i>	74	< 20 m	Cords (1990)
			<i>Cercopithecus ascanius</i>	<i>Cercopithecus mitis</i>	49		
	Gabon	Makokou	<i>Cercopithecus cephus</i>	All species combined	25	Not specified	Gautier-Hion et al. (1983)**
				<i>Cercopithecus nictitans</i>	25		
				<i>Cercopithecus pogonias</i>	25		
			<i>Cercopithecus nictitans</i>	<i>Cercopithecus pogonias</i>	100		
			<i>Cercopithecus pogonias</i>	<i>Cercopithecus nictitans</i>	100		
	Cote d'Ivoire	Taï	<i>Cercopithecus campbelli</i>	All species combined	95	When other species was within the spread of	Buzzard (2010)*
				<i>Cercopithecus diana</i>	89		
				<i>Procolobus verus</i>	75		
				<i>Procolobus badius</i>	55		
				<i>Colobus polykomos</i>	12		
				<i>Cercocebus atys</i>	15		



Region	Country	Site	Focal species	Species encountered	% association	Criterion	Reference
			<i>Cercopithecus petaurista</i>	All species combined	92	spread of the focal group	
				<i>Cercopithecus diana</i>	77		
				<i>Procolobus verus</i>	67		
				<i>Procolobus badius</i>	63		
				<i>Colobus polykomos</i>	20		
				<i>Cercocebus atys</i>	20		
	Cote d'Ivoire	Taï	<i>Procolobus badius</i>	<i>Cercopithecus diana</i>	66	< 50 m	Holenweg et al. (1996)
	Cote d'Ivoire	Taï	<i>Cercocebus atys</i>	<i>Cercopithecus diana</i>	10	Not specified	McGraw & Bshary (2002)
	Sierra Leone	Tiwai	<i>Cercopithecus diana</i>	<i>Procolobus badius</i>	5		
				All species combined	64	< 50 m	Whitesides (1989)**
				<i>Procolobus verus</i>	49		
				<i>Colobus polykomos</i>	15		
				<i>Cercopithecus petaurista</i>	9		
				<i>Procolobus badius</i>	8		
				<i>Cercopithecus campbelli</i>	4		
				<i>Cercocebus atys</i>	1		
Americas	Brazil	Río Blanco	<i>Saguinus mystax</i>	<i>Saguinus fuscicollis</i>	72	< 20 m	Heymann (1990)
	Bolivia	Pando	<i>Saguinus fuscicollis</i>	<i>Saguinus mystax</i>	82		
			<i>Saguinus labiatus</i>	<i>Saguinus fuscicollis</i>	75	< 50 m	Buchanan-Smith (1999)
			<i>Saguinus imperator</i>	<i>Saguinus fuscicollis</i>	59		
			<i>Saguinus fuscicollis</i>	<i>Saguinus labiatus</i>	75		
				<i>Saguinus imperator</i>	62		
	Brazil	Southern Bahia	<i>Leontopithecus chrysomelas</i>	<i>Callithrix kuhlii</i>	31	< 50 m	Oliveira & Dietz (2011)
	Brazil	River	<i>Saimiri sciureus</i>	<i>Chiropotes satanas</i>	20	< 50 m	Pinheiro et al. (2011)
		Tocantins, River		<i>Cebus apella</i>	10		
		Tocantins, River	<i>Saimiri sciureus</i>	<i>Cebus apella</i>	55		
		Tocantins, Germoplasm a Island		<i>Chiropotes utahickae</i>	3		
Asia	Malaysia	Danum Valley	<i>Presbytis rubicunda</i>	All species combined	6	< 50 m	This study

Region	Country	Site	Focal species	Species encountered	% association	Criterion	Reference
				<i>Pongo pygmaeus</i>	3		
				<i>Macaca fascicularis</i>	2		
				<i>Hylobates muelleri</i>	1		
				<i>Macaca nemestrina</i>	1		
	India	Nelliyampathy	<i>Macaca silenus</i>	All species combined	5	< 30 m	Erinjery et al. (2016)
				<i>Macaca radiata</i>	2		
		Anamalai	<i>Macaca silenus</i>	<i>Semnopithecus johnii</i>	3		
				All species combined	3		
				<i>Macaca radiata</i>	2		
				<i>Semnopithecus johnii</i>	<1		
Madagascar		Ampamelonabe	<i>Eulemur coronatus</i>	<i>Eulemur fulvus</i>	16	< 20 m	Freed (2007)
			<i>Eulemur fulvus</i>	<i>Eulemur coronatus</i>	12		

When multiple values were available for different seasons, we showed the mean.

\*We read figures from the graph so the values are not exact.

\*\*Mean of the two groups.