



Mouse Lemurs in an Assemblage of Cheirogaleid Primates in Menabe Central, Western Madagascar – Three Reasons to Coexist

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OPEN ACCESS

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Specialty section:

This article was submitted to
Population and Evolutionary
Dynamics,
a section of the journal
Frontiers in Ecology and Evolution

Received: 21 July 2020

Accepted: 22 February 2021

Published: 22 March 2021

Citation:

Schäffler L, Kappeler PM and
Halley JM (2021) Mouse Lemurs in an
Assemblage of Cheirogaleid Primates
in Menabe Central, Western
Madagascar – Three Reasons
to Coexist.
Front. Ecol. Evol. 9:585781.
doi: 10.3389/fevo.2021.585781

Ecological communities are structured by interactions between coexisting species that mutually influence their distribution and abundance. Ecologically similar species are expected to exclude one another from suitable habitat, so the coexistence of two mouse lemur species in an assemblage of several closely related cheirogaleid primates in the central Menabe region of Madagascar requires explanation. We assessed the occurrence of Madame Berthe's mouse lemurs (*Microcebus berthae*) and Gray mouse lemurs (*Microcebus murinus*), and of two larger cheirogaleids, Coquerel's giant mouse lemur (*Mirza coquereli*) and the western fat-tailed dwarf lemur (*Cheirogaleus medius*), by nocturnal line transect walks between 2003 and 2007. We explored interspecific interactions for four different scenarios with varying resource availability (degraded and non-degraded habitat in the wet and dry season), both on the regional spatial scale and on a finer local (transect) scale. We tested whether the interspecific distribution of mouse lemur individuals indicates interspecific competition and whether their regional coexistence might be stabilized by interactions with *M. coquereli* or *C. medius*. We developed the "Inter-Species Index of Attraction" (ISIA) to quantify the observed interspecific interactions within transects and determined if these were significantly different from a null model generated by a combination of randomization and bootstrapping to control for intraspecific aggregation. For the two mouse lemurs, interspecific spatial exclusion was most pronounced during the resource-poor dry season, consistent with the hypothesis of feeding competition. Seasonally varying distribution patterns indicated resource tracking in a spatio-temporally heterogeneous environment. The interspecific distribution of individuals suggested that the larger cheirogaleids benefit *M. berthae* at the expense of the more abundant *M. murinus*: spatial associations of both, *M. coquereli* and *C. medius*, with *M. murinus* were negative in most scenarios and across spatial scales, but neutral or even positive with *M. berthae*.

Thus, our study revealed that coexistence among ecologically similar heterospecifics can rely on complex density-mediated interspecific processes varying with habitat quality and season. With regard to the stability of animal assemblages, this insight has major implications for biodiversity conservation.

Keywords: ecological structure, community ecology, interspecific coexistence, competitive exclusion, intraguild predation, lemurs, dry deciduous forest, western Madagascar

INTRODUCTION

The ecological structure of communities is determined by a combination of abiotic and biotic factors (Polis, 1994; Stokstad, 2009). Complex relationships between consumers and resources affect food web dynamics both “top-down” and “bottom-up” (Polis and Strong, 1996; Leibold et al., 1997). Interspecific interactions between and within trophic levels structure ecological communities (Diamond, 1975) either directly between species (Lawton and Hassell, 1981) or indirectly (Strauss, 1991) if pairwise interactions are influenced by a third species (Bonsall and Hassell, 1997). According to the competitive exclusion principle, a pair of species with identical ecological demands cannot coexist (Hardin, 1960). Even if there is no universal limit to the similarity of competing species (Abrams, 1983), congeneric species should be engaged in intense competition (Sfenthourakis et al., 2006) and their coexistence in taxonomic assemblages (*sensu* Pianka, 1973) requires explanation.

Several mechanisms can stabilize the coexistence of closely related species with similar ecological demands (Chesson, 2000b), with the following being most relevant to our study. First, heterogeneity of the environment and differential responses of species to this variability facilitates coexistence (Levin, 1992). Competitive superiority of a species in certain habitat types may lead to local exclusion of inferior competitors, but coexistence can still be favored on a regional scale if spatio-temporal heterogeneity provides the outcompeted species with refuges (Amarasekare, 2003; López-Gómez and Molina-Meyer, 2006). Second, indirect interactions in species assemblages may weaken the intensity of direct interactions such as competition, and thus stabilize coexistence (Glasser, 1979; Holt, 1984; Ashehoug and Callaway, 2015).

Predation-risk may influence the decision of animals to avoid high-risk areas, which may have benefits for other community members (Willems and Hill, 2009; Bidner, 2014). If a predator favors the competitively superior species, either via specific preference or density dependence (Holt and Lawton, 1994; Chesson, 2000b), it reduces the relative abundance of the preferred prey (Sundell et al., 2003). This may indirectly benefit the competitively inferior prey species and prevent interspecific exclusion in assemblages of resource-limited consumers (Paine, 1966; Caswell, 1978; McPeck, 2014). Such changes of the competitive landscape (“keystone predation”: Paine, 1969) can have strong consequences for species richness (Walsh, 2013; Bidner, 2014). Shared natural enemies may lead to competition among prey for enemy-free space, generating spatial patterns resembling those of direct competition (“apparent competition”:

Holt, 1977; Bonsall and Holt, 2003). Two species with dietary niche overlap and shared predation risk may outcompete each other in different tasks and spatially segregate into most productive habitats and predator-free space (Chesson, 2000a,b). Finally, if predator and prey belong to the same trophic guild, they may simultaneously affect each other by both direct competition and predation (“intraguild predation”: Polis et al., 1989; Polis and Holt, 1992; Holt and Polis, 1997).

Global patterns of species co-occurrence suggest that primate communities are not randomly structured (Bourlière, 1985; Kamilar, 2009). Primary productivity and interspecific competition have been the major foci in primate community ecology (Schreier et al., 2009; Kamilar and Ledogar, 2011), whereas the effects of predation remain largely neglected (Bidner, 2014). Positive interactions among other terrestrial vertebrates have long been recognized (Terborgh, 1990; Dickman, 1992; Stensland et al., 2003) but remain underacknowledged as determinants of species co-occurrence (Stachowicz, 2001; Bruno et al., 2003; Denis et al., 2019). Studies on costs and benefits of mixed-species associations in primates are numerous, but they largely focused on large-bodied, diurnal, and gregarious haplorrhines (e.g., Heymann and Buchanan-Smith, 2000; Buzzard, 2010; Singh et al., 2011). Thus, additional studies from different primate lineages, in particular strepsirrhines, are needed to test the above-mentioned predictions about community composition and stability.

Lemurs make up about 20% of the global primate species richness (Estrada et al., 2017) and represent more than 60% of mammalian genera in Madagascar (Ganzhorn, 1999). Interspecific competition in lemurs is therefore likely strong (Kamilar and Guidi, 2010; Beaudrot and Marshall, 2011). The non-random checkerboard distribution of frugivore-insectivore (omnivore) lemur species in western Madagascar indeed suggests high levels of interspecific competition for food (Kamilar and Ledogar, 2011). However, based on differences in lemur body size and dietary niches, Schreier et al. (2009) challenged the assumption of a high number of competing species pairs in Madagascar and called for studies comparing simulated distribution patterns with observed community structure to highlight species competing within assemblages. A majority of studies that have investigated habitat utilization and feeding habits of co-occurring lemur species to date were conducted on single study sites (e.g., Rendigs et al., 2003; Schwab and Ganzhorn, 2004; Dammhahn and Kappeler, 2008a,b, 2014; Rakotondravony and Radespiel, 2009; Rakotondranary and Ganzhorn, 2012). We therefore aim at examining the interspecific spatial distribution in a community of nocturnal lemurs throughout the entire area of coexistence.

A taxonomic assemblage of four closely related lemur species of the cheirogaleid family (Lemuriformes: Cheirogaleidae) affords opportunity to study spatial consequences of interspecific interactions: the mouse lemurs *Microcebus berthae* and *Microcebus murinus*, the closely related giant mouse lemur *Mirza coquereli* and dwarf lemur *Cheirogaleus medius* are nocturnal, arboreal, and relatively small primates endemic to Madagascar (average adult masses of 31 g in *M. berthae* and 60 g in *M. murinus*; Schmid and Kappeler, 1994; Rasoloarison et al., 2000, 120 g in *C. medius*; Fietz, 2003, and 250 g in *M. coquereli*; Kappeler, 2003). These cheirogaleid species occur sympatrically in the dry forest of the central Menabe region in western Madagascar that is subject to both, spatial and temporal heterogeneities.

The restricted biogeographic range of *M. berthae* is confined to Menabe Central (Rasoloarison et al., 2000; Schwab and Ganzhorn, 2004), and its low disturbance tolerance indicate ecological specialization (Schäffler, 2012; Schäffler and Kappeler, 2014a). Its sympatric congener *M. murinus*, in contrast, is found throughout western and southern Madagascar and regionally co-occurs with several other mouse lemur species (Weisrock et al., 2010). The wide biogeographic distribution of *M. murinus* was explained by its high competitive potential, seasonal plasticity in feeding habits, efficient energy-saving strategies, and behavioral flexibility in habitat selection (Radespiel, 2016). In western Madagascar, *M. murinus* inhabits degraded forest parts and even village environments (Ganzhorn, 1987; Dammhahn and Kappeler, 2008a; Schäffler, 2012; Schäffler et al., 2015). Mouse lemurs are omnivorous (or more specifically fauni-frugivorous; Steffens and Lehman, 2016) but the feeding niche of *M. berthae* is narrower than that of *M. murinus* (Dammhahn and Kappeler, 2008a, 2010). To cope with seasonal fluctuations in food supply (Schwab and Ganzhorn, 2004) mouse lemurs rely on sugary secretions of homopteran larvae (genus *Flatidia*) as a key fallback food (Dammhahn and Kappeler, 2008a). Increased home range sizes of females in areas of co-occurrence indicated interspecific competition on a local scale (Dammhahn and Kappeler, 2009) and negative interspecific association patterns of populations were also observed on a regional scale (Schäffler et al., 2015).

The mouse lemurs are likely also engaged in interspecific interactions with the other two sympatric cheirogaleids (Hladik et al., 1980; Lahann, 2008). Stable isotope analyses of the cheirogaleid species in Menabe Central suggested that interspecific competition determined ecological structure in this species assemblage (Dammhahn and Kappeler, 2014). In Menabe Central, *M. coquereli* occurs in relatively low population densities and is heterogeneously distributed whereas *C. medius* was found in higher numbers in intact habitat than in degraded forest parts (Schäffler and Kappeler, 2014b). Opportunistic (intraguild) predation by *M. coquereli* was observed on *M. murinus* (Rakotonirainy, 2003; Schliehe-Diecks et al., 2010) but remains un-reported on *M. berthae*. Corresponding negative associations of *M. coquereli* and *M. murinus* and spatial overlaps between *M. coquereli* and *M. berthae* were documented at the population level (Schäffler et al., 2015). While *C. medius* hibernates throughout the dry season (Dausmann et al., 2004), *M. murinus* females enter daily and/or prolonged torpor to save

energy (Schmid, 1998, 2000, 2001). *Microcebus murinus* and *C. medius* compete for tree holes used for resting and breeding (Ganzhorn and Schmid, 1998; Kappeler and Rasoloarison, 2003) and there is evidence for feeding niche overlap in south-eastern Madagascar (Lahann, 2007). In contrast, *M. berthae* is active throughout the dry season (Schmid and Kappeler, 2005) and rests in open vegetation (Dammhahn and Kappeler, 2005). In a small-scale study, *C. medius* was found to partially displace *M. murinus*, whereas positive spatial associations with *M. berthae* indicated relaxed competition (Schwab and Ganzhorn, 2004).

Ecological patterns emerge from biological mechanisms that operate at different scales: the structure of communities may be imposed by large scale constraints but decisions to spatially avoid or associate with a co-occurring species are made by individuals responding to variations in intra- and interspecific densities (Levin, 1992). In lemurs, competitor and predator recognition is based on acoustic, visual, and olfactory cues: far-reaching acoustic signals and long-lasting odors enable recognition of other individuals over greater distances and longer timespans than visual cues, and olfactory signals are of particular importance to nocturnal arboreal lemurs under poor visibility (Klopfer, 1977). Thus, mouse lemur communication by acoustic and olfactory signals (Braune et al., 2005) should facilitate interspecific recognition. They can also be assumed to recognize other cheirogaleids not only in their immediate vicinity: *M. coquereli* is easily detectable by a variety of vocalizations, and olfactory signals likely facilitating its recognition as a potential predator (Kappeler, 2003). *Microcebus* spp. were shown to respond to olfactory cues of mammalian predators, presumably based on metabolites of meat digestion (Deppe et al., 2007; Sündermann et al., 2008; Kappel et al., 2011; Deppe and Kushnick, 2020). *Cheirogaleus medius* can be recognized by mouse lemurs by its frequent olfactory markings of territorial borders (Fietz, 1999b).

In this study, we aimed at further elucidating determinants of ecological structure in this cheirogaleid species assemblage by linking patterns observed at the population level (Schäffler et al., 2015) to the distribution of individuals. The hypothesized coexistence-stabilizing mechanism operates on the local scale (Huston, 1999), so the interspecific distribution of individuals should reflect competitive or predator-prey interactions. We investigated the distribution of cheirogaleid individuals across spatio-temporal heterogeneities to scrutinize if and under which constraints co-occurring dwarf and giant mouse lemurs may stabilize competitive mouse lemur coexistence. Against this background, we examine the following questions and hypotheses:

1. Do interspecific spatial distributions of individuals reflect competition between the two mouse lemur species? If there is intense competition between *M. murinus* and *M. berthae*, as indicated by previous small-scale studies (Schwab and Ganzhorn, 2004; Dammhahn and Kappeler, 2008a,b, 2009, 2010), we expect to observe strong spatial exclusion between these two species (H1a). Interspecific distribution patterns of individuals do not allow for conclusions about the direction of spatial displacement, but evidence from different regions in Madagascar suggests that *M. murinus* has a higher competitive potential than its sympatric sister species (Dammhahn and Kappeler, 2008b;

Rakotondranary et al., 2011; Thorén et al., 2011a). If competition is for food, interspecific avoidance should be most pronounced under resource scarcity, i.e., during the dry season (H1b) and in degraded habitat (H1c).

2. Does intraguild predation by *M. coquereli* on *M. murinus* stabilize competitive coexistence between the two mouse lemur species? If (intraguild) predation creates refuges for *M. berthae* from competition with its congener as interpreted based on the interspecific distribution of cheirogaleid populations observed in non-degraded habitat during the dry season (Schäffler et al., 2015), spatial avoidance of *M. coquereli* by *M. murinus* should be reflected in the distribution of individuals. As giant mouse lemur predation on mouse lemurs has only been reported on *M. murinus* (Schliehe-Diecks et al., 2010), we expect strong spatial exclusion between this species and *M. coquereli* (H2a), but not between *M. berthae* and *M. coquereli* (H1b). Negative spatial association of *M. coquereli* and *M. murinus* individuals should be particularly pronounced during the dry season when resource scarcity ought to favor opportunistic predation (H2c).

3. Does *C. medius* stabilize competitive mouse lemur coexistence by spatial exclusion of *M. murinus*? Partial displacement of *M. murinus*, but not *M. berthae*, suggested that *M. berthae* would develop large subpopulations where *C. medius* reduces habitat suitability for *M. murinus* (Schwab and Ganzhorn, 2004). This hypothesis was not supported by the distribution of mouse lemur populations in relation to the occurrence of *C. medius* (Schäffler et al., 2015) but may still be reflected by the distribution individuals across spatio-temporal heterogeneities. Therefore, we predict a negative association between *C. medius* and *M. murinus* (H3a) but not between *C. medius* and *M. berthae* (H3b). Spatial consequences of competition between *M. murinus* and *C. medius* should be strongest when resources are scarce (H3c). With respect to food, spatial avoidance would be expected predominately in degraded habitat. Competition for tree holes should be more pronounced in non-degraded habitat with more old-growth trees and high *C. medius* population densities.

MATERIALS AND METHODS

Study Site

The region of Menabe Central ranges from the Mozambique Channel to the bottom of the central highlands and is bound by the rivers Tsiribihina to the north and Morondava to the south. With approximately 65,000 hectares of forested area at the time of our surveys, Menabe Central retained the largest remnant of dry deciduous forest in western Madagascar (Sorg et al., 2003). Varying levels of anthropogenic pressure fragmented the forest and resulted in a mosaic of different vegetation forms between and within major fragments (Smith et al., 1997; see also Figure 4 in Online Resource 2). The climate is classified as tropical dry with a distinct dry season between March and November and a hot wet season with heavy rains peaking from December to February (Sorg and Rohner, 1996). Slash and burn agriculture and illegal logging are continuously degrading the forest in Menabe Central. The northernmost forest part

Ambadira still contained considerable areas of near primary forest with moderate anthropogenic disturbance levels (Smith et al., 1997). In Kirindy Forest further south, exploitation has been limited by a silvicultural concession (Ganzhorn et al., 1990) and the research station of the German Primate Center (Sorg et al., 2003). Largely unrestricted forest utilization in other parts of Menabe Central have segregated Ambadira and Kirindy and the narrow corridor connecting them is highly frequented by rural people. The southernmost forest part in the Reserve Spécial Andranomena has been prone to clearing and degradation for decades despite governmental protection (Smith et al., 1997; Randrianandianina et al., 2003).

Line Transect Sampling

We sampled sites across the area of occurrence of the four cheirogaleid species in the Menabe Central region in western Madagascar (boundaries north 44°37'E, 19°44'S; south 20°13'S, 44°38'E). To account for temporal heterogeneity, we conducted surveys during both the warm and resource-rich wet season and the cooler dry season (Sorg et al., 2003). We distributed 34 line transects of 1 km length as randomly as possible in the dense dry deciduous forest and categorized the habitat they were in as either non-degraded or degraded (for details on sampling design and habitat assessment, see Schäffler et al., 2015 and **Supplementary Figure 4**).

We surveyed cheirogaleid species by repeated transect walks over four dry seasons (3 months, respectively, between July and September in 2003, 2004, 2006, and 2007) and two wet season surveys (February to April and November to December in 2007). During each survey, cheirogaleid occurrence was determined on 13–23 of the 1 km line transects by distance sampling (Buckland et al., 2001, 2010). The majority of 34 dry-season and 26 wet-season line transects were walked twice or three times over subsequent surveys, amounting to a total of 127 transect walks of 1 km. Two observers trained to recognize cheirogaleids in their natural habitat at night walked with headlights along the line transects at a standardized pace of about 1 km/h between 6:00 pm and 8:30 pm. Using torches and binoculars, individuals were visually detected and identified to the species level. While *C. medius* and *M. coquereli* are relatively easy to recognize, also at greater distances, distinction of the two mouse lemur species requires skilled eyes. Both observers were trained in discriminating *M. berthae* from *M. murinus* by its considerably smaller size and longer tail, as well as its more gracile body and facial shape with shorter ears (Schmid and Kappeler, 1994). Individuals located too far from the transect line for reliable identification were approached by the observers. Animals that could not be identified with confidence were excluded from subsequent analyses. Of the 786 *Microcebus* sightings, 92 were *M. berthae* (11,7%), 514 *M. murinus* (65,4%), and 180 individuals could not be identified to species level (22,9%). The perpendicular distance of detected animals from the transect line was estimated by both observers independently to warrant reliability (Buckland et al., 2001); if no agreement was reached, we measured the distance by step length. Laser range finders were of limited use in the forest, particularly during the wet season with dense foliage. The number of detections declined with increasing distance

from the transect line in the same way for identified and non-identified *Microcebus* individuals. Positions along transects were determined with a Garmin GPSmap 60CSx device providing high positioning accuracy under a closed canopy and controlled by flags fixed on trees every 25 m.

Analysis of the Interspecific Distribution of Individuals

The analysis in this paper is designed to investigate the associations between different pairs of species at two different scales. On the coarse or “regional” scale, we considered the simple correlations between counts of individuals from different species across the array of transect walks on the basis of Spearman’s rank correlation. For the finer or “local” scale, we considered the aggregation or segregation between individuals within transects, using an “Inter-Species Index of Attraction” (ISIA). A flow chart showing the statistical analyses is given in Online Resource 1.

Regional Scale Calculation

We worked with the array of samples from the 127 transect walks. As some of these walks were conducted on the same transect, either in the same or in different years, we assumed that these repeated walks yielded independent observations (i.e., no temporal autocorrelation) and was dependent only on the time of year (i.e., dry or wet season). Our basic data were thus an array of observed individuals, including the observation number, walk number, scenario type (wet and dry season, degraded and non-degraded habitat), distance along transect, perpendicular distance from transect line and the species. This array was stored as an R data frame prior to running our analyses. Counting numbers of each species per transect walk yielded a matrix of observations of size 4×127 observations. We then calculated Spearman’s rank correlation coefficient for each pair of species over the array of transects. Although there are six possible heterospecific pairings, only five involve mouse lemurs. Spearman’s rank correlation coefficient ranges between -1 and $+1$, with a negative value indicating avoidance between two species and a positive value indicating attraction. Because it is a non-parametric statistic it is attractive in being robust against departures from statistical normality. We refer to this scale as “regional,” since each datum consists of the numbers of individuals for each species in each transect. This measures the possibly uneven occupation of different transects by different species on scales from 1 km (the length of a transect) to 13 m (transect width: Schäffler, 2012). The calculation of the Spearman coefficient and its p -value was carried out using “rcorr” function in the Hmisc package (Harrell and Dupont, 2020) in R (R Development Core Team, 2018).

Local Scale Calculation

We sought pairings of individuals by testing if they fell within the “recognition distance.” An encounter situation, or interaction, between two individuals is assumed to potentially occur when the distance separating them is less than this recognition distance. To our knowledge, recognition distances of cheirogaleids have not been previously investigated in detail although the general idea appears in various studies (Lima and Dill, 1990;

Hutchinson and Waser, 2007; Jackson and Fahrig, 2012). Our choice of 150 m as a recognition distance was based on the notion that this distance should be the same order as home range size. Because home range estimates for cheirogaleids vary with different methods of data collection and analysis (Sterling et al., 2000), range sizes are very variable both between and within species. We chose a value of 150 m that is close to the median home range diameter found in previous studies (Table 1). We were interested in patterns showing possible interactions between individuals of the same or of different species. For example, competitors should avoid each other, forming fewer pairs than expected by chance. In each transect, an observation of a lemur consisted of the species identity and its location. The census of pairings for a single individual included all pairings with heterospecifics and with conspecifics when the direct (Euclidian) distance of separation was less than the recognition distance of 150 m. There were four types of intraspecific pairings and six types of interspecific pairings. The census for the transect was the sum of distinct pairings summed over all individuals on the transect.

Having identified all pairs within the “recognition distance” on each transect walk, we pooled all results for each type of scenario. This yielded a second array consisting of observed pair numbers, scenario type and the two species identities. To calculate the correlation between any two species, “A” and “B,” we then used the following “Inter-Species Index of Attraction” index (ISIA, see Online Resource 1):

$$T(A, B) = 1 - \left(\sqrt{\frac{M_{AA}}{M_0}} + \sqrt{\frac{M_{BB}}{M_0}} \right)^2$$

Here M_0 is the total number of pairs involving species A and B only, while M_{AA} is the number of pairs involving two individuals both of species A, and M_{BB} is the number of pairs involving two individuals of species B. The index $T(A,B)$ is a measure of the degree on interspecific attraction between A and

TABLE 1 | Range of mean or median home range size estimates of both males and females in the focal cheirogaleid species as reported in the literature and corresponding diameter ranges.

Species	Home range size [ha]	Home range diameter [m]	Mean diameter [m]	References
<i>M. murinus</i>	0.26–4.90	51.0–221.4	136.2	Radespiel, 2000; Eberle and Kappeler, 2002, 2004; Dammhahn and Kappeler, 2009
<i>M. berthae</i>	2.04–4.92	142.8–221.8	182.3	Dammhahn and Kappeler, 2005, 2009
<i>C. medius</i>	1.40–3.93	118.3–198.2	158.3	Fietz, 1999a,b, 2003
<i>M. coquereli</i>	1.00–4.00	100.0–200.0	150.0	Kappeler, 1997, 2003 ^a

^aIncreased male home range size during the mating season not considered.

TABLE 2 | (A) Numbers of detected cheirogaleid individuals in the four scenarios.

	<i>Microcebus berthae</i>		<i>Microcebus murinus</i>		<i>Mirza coquereli</i>		<i>Cheirogaleus medius</i>	
	Dry season	Wet season	Dry season	Wet season	Dry season	Wet season	Dry season	Wet season
Non-degraded habitat	34	34	103	112	16	13	–	109
Degraded habitat	19	4	187	72	14	24	–	54

(B) Comparison of cheirogaleid detections between transects sampled twice, at the onset and at the end of the rainy season (Wilcoxon signed-rank test, $n = 16$).

Species	Z	P (two-sided)
<i>M. berthae</i>	–0.282 ^a	0.778
<i>M. murinus</i>	–1.649 ^a	0.099
<i>M. coquereli</i>	–0.213 ^a	0.832
<i>C. medius</i>	–0.747 ^b	0.455

^aBased on positive ranks.

^bBased on negative ranks.

B, relative to the expected value for purely random behavior. T is large when a transect has many interspecific pairs and few conspecific pairs. It has a minimum of $T = -1$ (avoidance) when $M_{AA} = M_{BB} = M_0/2$ while it has a maximum of $T = +1$ when $M_{AA} = M_{BB} = 0$ (attraction). For each of the five mouse-lemur interactions, we evaluated $T(A,B)$ for every transect walk that contained at least one individual of species A and B. Thus, for each of the five combinations, we obtained a single value of the index. While this statistic is a measure of aggregation or avoidance between two species, estimating the significance of this value requires a comparison with the distribution of values in a null model. Thus, for each of the five combinations, we compared the observed value of ISIA with values it takes in a randomized model.

To test the significance of T (avoidance or attraction) we created a null model by a combination of randomization and bootstrapping, assuming that there are no interspecific interactions. Such null models have been generated by various methods (Ulrich and Gotelli, 2010). In this study, we used an approach similar to the “ideal gas model” (IGM: Hutchinson and Waser, 2007). As we aimed specifically to measure attraction or repulsion between individuals of different species, the null distribution should preserve overall levels of clustering but be neutral with respect to species. Randomization by retaining all observations in space and only shuffling species identities, however, fails to account for interspecific differences in long-range visibility. To solve this issue, we treated distances along transects (x-distances) and perpendicular distances (y-distances) separately. For any given walk, a random resample of x-distances was found by shuffling species identities randomly among the observed positions on that walk. All the y-distances were pooled for each species to provide a distribution of perpendicular distances. Random sampling from this distribution with replacement, as in the bootstrap method, provided the corresponding y-distances (see Online Resource 1 for details on the null model). Repeating the randomization K times yields K values of T . This method is sensitive to avoidance or aggregation between species within walks and can detect segregation at a very local scale even when there is some aggregation (e.g., because of shared habitat preferences) common to all species.

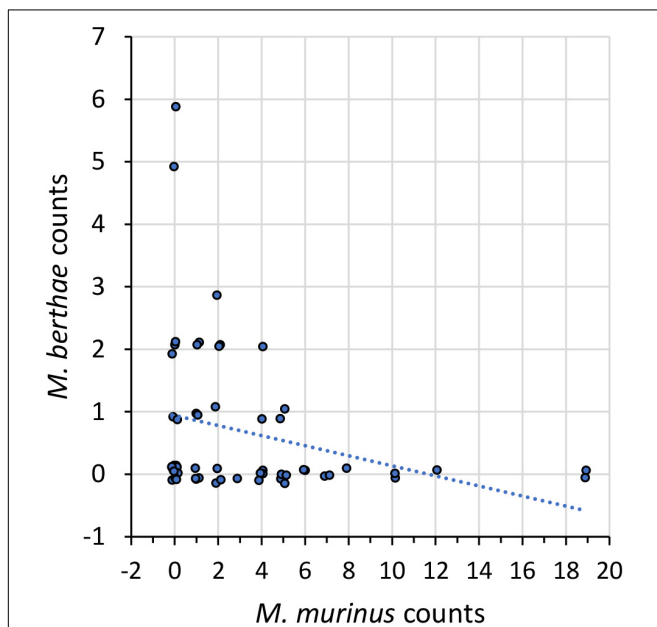
To exclude a potential bias caused by the emergence of juveniles at the end of the breeding season or by detectability varying for behavioral reasons between the onset and the end of the wet season, we compared the number of detected individuals between 16 transects sampled during both, early and late rainy season using a Wilcoxon signed-rank test. Variations in resource supply between the dry and the wet season are self-explaining. Disturbed forests differ in abiotic and biotic characteristics from intact habitats and lemurs show divergent responses in microhabitat selection (Ganzhorn et al., 1997; Ganzhorn and Schmid, 1998; Lehman et al., 2006a,b,c; Burke and Lehman, 2014; Lehman, 2016; Andriatsitohaina et al., 2020), so habitat degradation should indirectly affect species interactions. Thus, we divided the data into four “scenarios”: (1) dry season – non-degraded habitat, (2) dry – degraded, (3) wet – non-degraded, and (4) wet – degraded. All calculations were repeated on these four datasets to see if the correlations changed between seasons and habitat types and were carried out in R.

RESULTS

We observed a total of 794 lemurs over the entire survey period. The most common species in both seasons was *M. murinus*, with 473 individuals. This is much greater than for *M. berthae* with 91 or *M. coquereli* with 67 total observations. In the wet season, *C. medius* was the second most common species with 163 observations. In non-degraded forest parts of Menabe Central, trees grew taller and in higher densities with a more closed canopy cover than in degraded habitat (Schäffler et al., 2015). More lemurs were observed in non-degraded habitats ($n = 421$) than in degraded habitats ($n = 373$). Numbers of detected individuals per species did vary with spatio-temporal heterogeneities in that more mouse lemurs were observed in degraded habitat during the dry season (Table 2A), whereas there was no difference between early and late rainy season counts in any species (Table 2B). In most cases, the number of inter- and intraspecific pairs of individuals within 150 m was higher in degraded habitat during the dry season, whereas more pairs were observed within recognition distance in non-degraded habitat during the rainy season (Table 3).

TABLE 3 | Number of transect walks per scenario as well as the numbers of inter- and intraspecific pairs of individuals detected within 150 m on single transect walks.

	Dry season		Wet season		Sum of pairs
	Non-degraded	Degraded	Non-degraded	Degraded	
Number of transect walks	37	34	33	23	
Interspecific pairs					
<i>M. berthae</i> - <i>M. murinus</i>	9	22	12	0	43
<i>M. berthae</i> - <i>M. coquereli</i>	8	6	3	2	19
<i>M. berthae</i> - <i>C. medius</i>	–	–	42	4	46
<i>M. murinus</i> - <i>M. coquereli</i>	0	7	3	6	16
<i>M. murinus</i> - <i>C. medius</i>	–	–	69	34	103
<i>M. coquereli</i> - <i>C. medius</i>	–	–	15	7	22
Intraspecific pairs					
<i>M. berthae</i>	15	12	7	1	35
<i>M. murinus</i>	95	254	160	43	552
<i>M. coquereli</i>	3	4	1	7	15
<i>C. medius</i>	–	–	99	24	123

**FIGURE 1** | Spatial association of *M. berthae* with *M. murinus*. Scatter plot shows the numbers of *M. berthae* sighted within a transect walk as a function of those of *M. murinus* on the same walk for all transect walks. Points have been modified by a small uniform jitter in each coordinate ($SD = 0.144$) to visualize multiple observations, while the dotted line is the least-squares fit (provided only as a visual aid, it is not a regression line as data are not normally distributed). These counts represent data pooled over all scenarios. The figures corresponding to each of the four scenarios for *M. murinus* and *M. berthae* can be found in Online Resource 2.

To test the first set of hypotheses (H1), we investigated whether there is evidence of avoidance between *M. murinus* and *M. berthae*. Results in **Table 4A** and **Figure 1** (see also **Supplementary Figure 1** in Online Resource 2) clearly showed a tendency for mutual exclusion, supporting Hypothesis 1a, as nine of the ten indices (ρ and T) are negative, although only

three of these values were statistically significant. The pooled data showed significant evidence of segregation at both scales. At the local scale, there was segregation during the dry season in non-degraded habitat supporting Hypothesis 1b, but no evidence of segregation in the degraded habitats and thus no support for Hypothesis 1c.

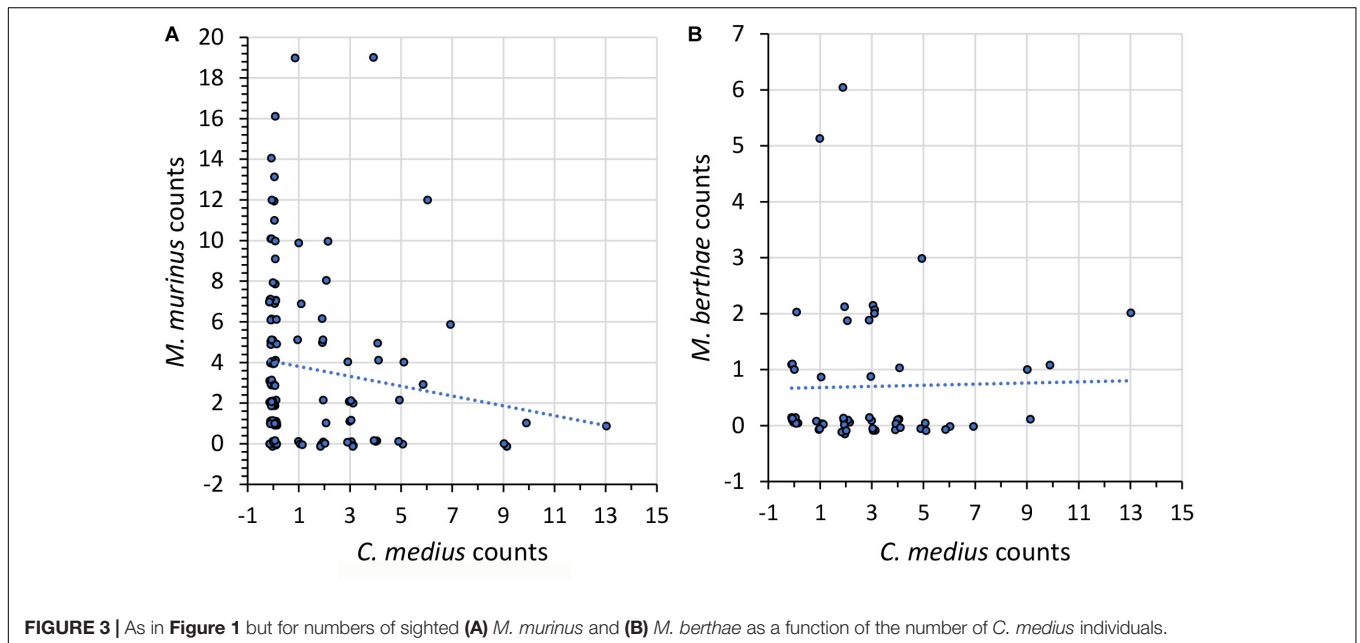
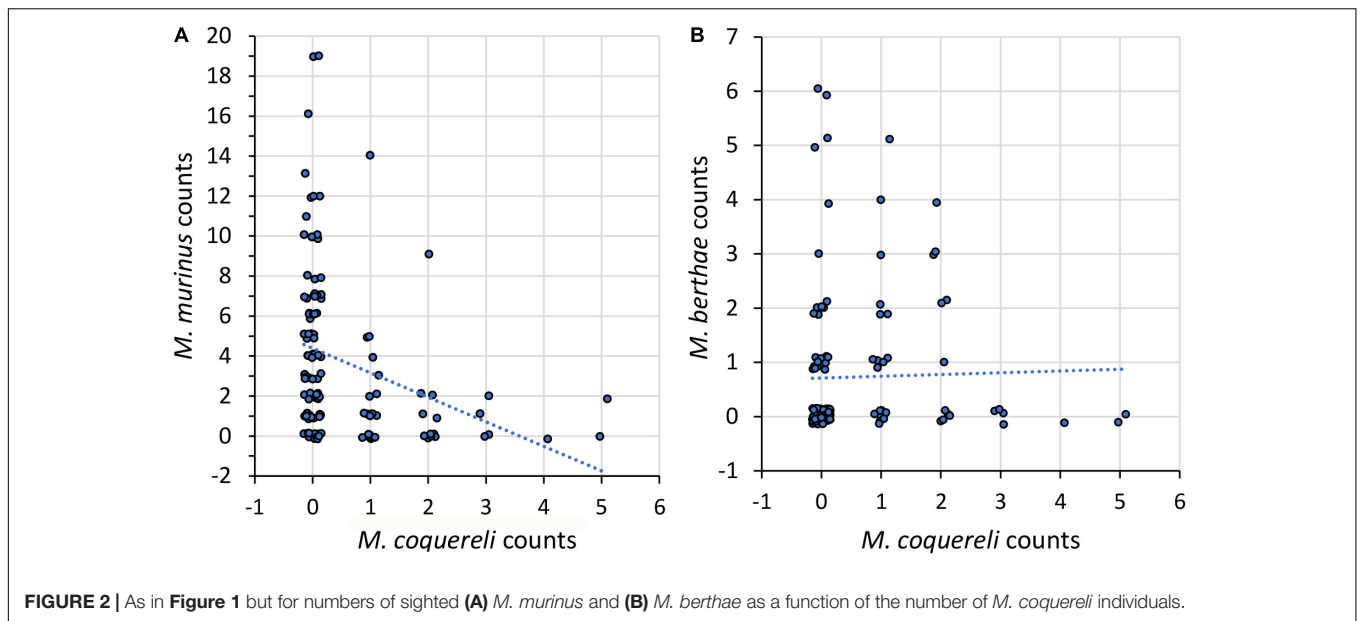
Hypothesis 2a predicted segregation between *M. murinus* and *M. coquereli*, which was observed at the regional scale in the pooled data (**Figure 2A**) and in all scenarios but in degraded habitat during the dry season (**Table 4B** and **Supplementary Figure 2A**). In contrast, no segregation was observed between *M. berthae* and *M. coquereli* (**Table 4B** and **Figure 2B**), complying with Hypothesis 2b. On the regional scale, those two species were even positively associated in degraded habitat during the dry season (**Supplementary Figure 2B**). Negative spatial association of *M. murinus* and *M. coquereli* within transects was limited to the dry season with food scarcity (**Supplementary Figure 2A**) and thus conforms with Hypothesis 2c.

Segregation patterns found between *M. murinus* and *C. medius* complied with Hypothesis 3a (**Table 4C** and **Figure 3A**). Lack of avoidance between *M. berthae* and *C. medius* on the regional scale (**Table 4C** and **Figure 3B**) and attraction within transects in non-degraded habitats (**Supplementary Figure 3B**) supported Hypothesis 3b. Segregation of *M. murinus* and *C. medius* was detected at the regional level in non-degraded habitat (**Supplementary Figure 3A**) and within transects in degraded habitat, which indicates both competition for tree holes and food according to Hypothesis 3c.

DISCUSSION

Competition Between *Microcebus* spp.

Mouse lemur coexistence appears to be stabilized by avoidance of heterospecific individuals and movements in a spatio-temporally varying environment. Spatial segregation between the mouse lemurs was indicated by the pooled data at the regional and



local scale. During the dry season, the distribution pattern of individuals within transects also indicated interspecific avoidance, with significant results in non-degraded habitat and a non-significant trend in degraded habitat. These results generally support the notion of spatial exclusion, which is in line with the conclusion of previous studies that mouse lemur differentiation in feeding niches and microhabitat utilization was insufficient to prevent competitive exclusion when resources are scarce (Ganzhorn and Kappeler, 1996; Schwab and Ganzhorn, 2004; Dammhahn and Kappeler, 2008b, 2009, 2010). Coexistence in a spatially heterogeneous competitive environment was also considered a probable explanation for the co-occurrence of closely related mouse lemur species in north-western Madagascar (Rakotondravony and Radespiel, 2009).

However, mouse lemur association did not meet the prediction that spatial segregation should be particularly pronounced in degraded habitat. Small-sized nocturnal lemurs have evolved specific adaptations to cope with the extremely seasonal dry forest habitats of western Madagascar. Female *M. murinus* enter torpor to save energy (Schmid and Kappeler, 2005), which reduces the number of animals competing for over limited food resources (Thorén et al., 2011b). Moreover, species escape intense interspecific competition over food by shifting their diets to fallback food: sugary secretions of homopteran larvae represent a key fallback food for *M. murinus* during the dry season, while *M. berthae* relies on this feeding resource year-round (Dammhahn and Kappeler, 2008a). Similar to *M. berthae* and *M. murinus*, feeding niche overlap

TABLE 4 | (A–C) Interspecific correlation coefficient for individual numbers on transects and index T (Eq. 1) measuring interspecific aggregation within transects for five species combinations and four different scenarios.**(A) Interspecific associations between the two mouse lemur species.**

Scenario	<i>M. berthae</i> - <i>M. murinus</i>			
	regional		within transects	
	ρ	<i>P</i>	<i>T</i>	<i>P</i>
Non-degraded habitat / dry season	-0.30	0.0708	-0.13	0.013*
Degraded habitat / dry season	-0.24	0.1657	-0.06	0.053
Non-degraded habitat / wet season	-0.29	0.0961	+0.06	0.849
Degraded habitat / wet season	-0.15	0.4971	-0.15	0.21
Pooled	-0.30	0.0005**	-0.05	0.045*

(B) Interspecific associations of mouse lemurs and *M. coquereli*.

Scenario	<i>M. berthae</i> - <i>M. coquereli</i>				<i>M. murinus</i> - <i>M. coquereli</i>			
	regional		within transects		regional		within transects	
	ρ	<i>P</i>	<i>T</i>	<i>P</i>	ρ	<i>P</i>	<i>T</i>	<i>P</i>
Non-degraded habitat / dry season	+0.16	0.3509	-0.07	0.292	-0.57	0.0002**	-0.11	0.040*
Degraded habitat / dry season	+0.35	0.0423*	-0.13	0.197	-0.22	0.2127	-0.08	0.001**
Non-degraded habitat / wet season	+0.09	0.6071	-0.02	0.548	-0.39	0.0232*	+0.02	0.788
Degraded habitat / wet season	+0.25	0.2547	-0.14	0.383	-0.58	0.0039**	-0.08	0.218
Pooled	+0.16	0.0731	-0.03	0.354	-0.43	0.0000**	-0.05	0.013*

(C) Interspecific associations of mouse lemurs and *C. medius*.

Scenario	<i>M. berthae</i> - <i>C. medius</i>				<i>M. murinus</i> - <i>C. medius</i>			
	regional		within transects		regional		within transects	
	ρ	<i>P</i>	<i>T</i>	<i>P</i>	ρ	<i>P</i>	<i>T</i>	<i>P</i>
Non-degraded habitat / wet season	-0.11	0.5495	+0.14	0.044*	-0.34	0.0500*	-0.07	0.053
Degraded habitat / wet season	+0.01	0.9776	-0.12	0.36	+0.10	0.6500	-0.21	0.011*
Pooled	+0.03	0.7771	+0.05	0.774	-0.21	0.0186*	-0.06	0.003**

" ρ " means Spearman's rank correlation coefficient. Asterisks mark significant (*) or highly significant (**) results. Spatial association or avoidance are indicated by positive or negative T -values.

between sympatric *Microcebus ravelobensis* and *M. murinus* in northwestern Madagascar was found to be reduced by slight differences in dietary composition: *M. ravelobensis* relies heavily on insect secretions whereas a higher feeding plasticity in *M. murinus* was indicated by more pronounced seasonal shifts (Thorén et al., 2011b).

Mouse lemur individuals were more frequently encountered in degraded habitat during the dry season compared to the wet season (Table 2A), possibly tracking homopteran larvae that occur in higher abundance along forest edges (Corbin and Schmid, 1995). In north-western Madagascar, capture rates of *M. ravelobensis* were also higher in edge habitats, where small insects were more abundant (Burke and Lehman, 2014). Higher availability of insect prey was also assumed to explain the positive edge response of *M. rufus* in the eastern Malagasy rain forest (Lehman et al., 2006a,c). The seasonal differences correspond to results of an earlier study showing that *M. murinus* extended their foraging efforts to a greater number of transects during the dry season whereas they concentrated on fewer transects during the wet season (Schäffler et al., 2015). The population of

M. berthae was largely confined to non-degraded habitat during the wet season but occupied also degraded habitats during the dry season. Habitat partitioning along anthropogenic disturbance gradients was indicated during the dry season in degraded habitat as *M. berthae* avoided anthropogenic environments, whereas *M. murinus* was found in close vicinity to villages (Schäffler et al., 2015). A greater flexibility in habitat selection may thus enable *M. murinus* to exclusively access resources, corresponding to a high ecological generalization that can also be concluded from *M. murinus* prevalence in a wide range of environments (Kamilar et al., 2016). However, there is evidence for divergent habitat selectivity in different parts of Madagascar. In north-western Madagascar, *M. murinus* was associated with older and less disturbed forests whereas sympatric *M. ravelobensis* showed more flexibility in habitat use with edge tolerance (Rendigs et al., 2003; Lehman, 2016) and occupied a greater proportion of habitat patches than *M. murinus* in a fragmented landscape (Steffens and Lehman, 2016). In the spiny forest of south-eastern Madagascar, *M. murinus* was found to prefer larger trees than *M. griseorufus* only where the mouse lemurs occurred in

sympatry, whereas habitat selectivity of either species was low in allopatric populations (Rakotondrany and Ganzhorn, 2012).

Mouse Lemur Interactions With *M. coquereli*

Both mouse lemurs should be affected by resource competition with *M. coquereli* during the dry season when all three species feed on homopteran secretions (Kappeler, 2003). We observed negative association of *M. coquereli* and *M. murinus* in most scenarios and across scales. The regional scale association of *M. berthae* and *M. coquereli* indicate that feeding competition is relaxed in degraded habitat during the dry season, probably due to high insect abundance in edge habitat (Burke and Lehman, 2014). Moreover, the feeding niches of *M. murinus* and *M. coquereli* are differentiated in fruit and animal matter (Dammhahn and Kappeler, 2014). As competition for food alone cannot explain the observed interspecific segregation, opportunistic predation by *M. coquereli* may be an additional cause for spatial avoidance (Schliehe-Diecks et al., 2010).

Interspecific mouse lemur distribution may thus be interpreted as the outcome of competition between individuals that simultaneously differ in their ability to exploit resources and their susceptibility to predation (Grand and Dill, 1999), i.e., as a consequence of “apparent competition” (e.g., Holt and Lawton, 1994). The contribution of predators to competitive coexistence of prey species varies with heterogeneity of predation risk in space and time, rather than with magnitude of the pressure (Kotler et al., 1994). As the superior competitor for enemy-free space, *M. murinus* can escape (intraguild) predation pressure during the dry season by seeking refuge in the vicinity of villages (Schäffler et al., 2015). In contrast, disturbance-intolerant *M. berthae* cannot avoid interspecific interactions with *M. coquereli* in intact habitat, but profits from reduced competition with the congener in refuges created by the giant mouse lemur.

It remains puzzling why only *M. murinus* appears to be affected by *M. coquereli*. One explanation would be a specific preference of *M. coquereli* for one mouse lemur over the other, but *M. murinus* may rather be more exposed to opportunistic predation than *M. berthae* due to its more clustered social organization (*M. murinus*: Eberle and Kappeler, 2002, 2004, 2006; Wimmer et al., 2002; *M. berthae*: Dammhahn and Kappeler, 2005, 2009; see also **Table 3**). Moreover, *M. murinus* occurs in higher population densities (180 individuals km⁻²) than *M. berthae* (80 individuals km⁻²; Schäffler, 2012), so it may be the more profitable prey for *M. coquereli* because there are simply more individuals available. Finally, the two mouse lemur species may respond differently to (intraguild) predators. Variation in sleeping site utilization between mouse lemur species was interpreted as an outcome of divergent anti-predator strategies. In *M. murinus*, females hiding in tree holes likely profit from reduced risk of detection by predators and from protected shelters, so females can even afford to sleep in kin groups (Radespiel et al., 1998, 2003). Male *M. murinus*, in contrast, most often rest alone in open vegetation, which may be the best predator-avoidance strategy when high-quality tree

holes are monopolized by females (Radespiel et al., 1998). In *M. berthae*, both sexes sleep in less protected sites such as leaf nests and rather rely on cryptic behavior by resting solitarily or occasionally in small sleeping associations (Dammhahn and Kappeler, 2005). The rapid escape response reported for *M. ravelobensis* that also sleeps in open vegetation (Radespiel et al., 2003) was not observed in *M. berthae*, which may instead pursue a more cryptic strategy to avoid detection by a predator. The biogeographic history of mouse lemurs may also explain their divergent avoidance behavior with respect to *M. coquereli*. With its presumed origin in the area of micro-endemism comprising Menabe Central (Wilmé et al., 2006; Weisrock et al., 2010) and its limited range entirely overlapping with that of *M. coquereli*, *M. berthae* may have evolved specific strategies to cope with the intraguild predator. In contrast, *M. murinus* also occurs in areas where *M. coquereli* is absent and the genetic population structure in north-western Madagascar indicated a rather recent range expansion (Schneider et al., 2010) from its presumed origin in south-western Madagascar (Yoder et al., 2000; Olivieri et al., 2007). Owing to less distributional overlap and a shorter history of coexistence, *M. murinus* may thus be less well adapted than *M. berthae* to intraguild-predation by *M. coquereli*.

Mouse Lemur Interactions With *C. medius*

The interspecific distribution of mouse lemur individuals during the wet season supports the hypothesis that *C. medius* also plays a central role in stabilizing competitive mouse lemur coexistence. Spatial segregation of *M. murinus* and *C. medius* contrasted with the positive association between *M. berthae* and *C. medius* in non-degraded habitat.

Interspecific segregation between *M. murinus* and *C. medius* in relation to habitat heterogeneity indicated both regional-scale competition for suitable tree holes that are predominately found in old growth forest (Schwab and Ganzhorn, 2004) and for food within transects. Similar to *Cheirogaleus major* that is more abundant in the rainforest interior with large trees than in edge habitat (Lehman et al., 2006a,c), *C. medius* occurs in highest population densities in non-degraded habitat and far from villages (Schäffler and Kappeler, 2014b). By colonizing anthropogenic environments, *M. murinus* may avoid agonistic interactions with the superior competitor for tree holes (Schwab and Ganzhorn, 2004; Schäffler, 2012; Schäffler et al., 2015). In contrast, interspecific avoidance between *M. murinus* and *C. medius* individuals within transects was most pronounced in degraded habitat, indicating feeding competition, the context in which *C. medius* was observed to outcompete *M. murinus* (Ganzhorn and Kappeler, 1996).

Spatial consequences of resource competition have also been reported in other lemur communities. Sympatric lemur species do not only compete within but also between functional groups (Ganzhorn, 1997), and even competition between taxa of different orders may determine the composition of species assemblages: the absence of *M. coquereli* and ecologically equivalent species in eastern Madagascar was suggested to result

not only from competition for fruit with *C. major*, but also from competitive exclusion by the carnivorous ring-tailed mongoose (*Galidia elegans*; Ganzhorn et al., 1999).

Positive spatial association of *M. berthae* and *C. medius* individuals agreed with our prediction that crowding in most productive habitats, where fruit and animal matter is highly abundant during the wet season, outweighs effects of interspecific competition caused by pronounced feeding niche overlap. Just as *C. medius*, *C. major* in the rain forest near Andasibe is only active during the hot season when young leaves, flowers and fruit are abundant and entirely overlaps in food and habitat utilization with the else well separated niches of co-occurring species (Ganzhorn, 1989). In addition, differential use of both, structural microhabitat features (Schwab and Ganzhorn, 2004) and sleeping sites (Fietz, 2003; Dammhahn and Kappeler, 2005), likely helps to avoid direct interference between *M. berthae* and *C. medius* and allows for positive spatial association of individuals in non-degraded habitat. Similar to *M. berthae*, *M. ravelobensis* uses open sleeping sites like lianas or leaf nests and does not compete for three holes that represent a critical resource for other cheirogaleids (Rendigs et al., 2003).

Mechanisms Stabilizing Competitive Coexistence

Spatial segregation patterns like those documented between *M. berthae* and *M. murinus* as well as between *M. murinus* and *C. medius* were frequently observed in other primates. Lemur assemblages in the Malagasy rain forests have even more sympatric species and co-occurring congeners than communities in the western dry deciduous forest (Ganzhorn et al., 1999). In the fragmented rain forest of Kianjavato, several cooccurring gregarious lemurs that are diurnal and frugivorous were found to reduce interspecific competition by segregating their core areas (Holmes et al., 2019). Similarly, spatial segregation of co-occurring primates in Indonesia (Tilson and Tenaza, 1982), Borneo (Rodman, 1973), and Guyana (Levi et al., 2013) were considered a consequence of interspecific competition. Agonistic behavior between sympatric species can cause spatial segregation and is often pronounced between species in taxonomic assemblages (Dempster and Perrin, 1990). While *C. medius* was reported to prevail over other cheirogaleids in contest competition (Ganzhorn and Kappeler, 1996; Ganzhorn et al., 1999), aggressive interactions between mouse lemurs at food resources are rather rare (Dammhahn and Kappeler, 2005; Thorén et al., 2016). However, spatial exclusion in coexisting species may also occur without conflicts if subordinate species use auditory or olfactory cues to detect and avoid dominant species that gain exclusive access to resource-rich microhabitats (Dickman, 1991; Rychlik and Zwolak, 2005).

Moreover, variations in habitat utilization and interspecific association patterns in a spatio-temporally heterogeneous environment likely facilitate mouse lemur coexistence. Many sympatric species change their feeding or ranging behavior in response to increased competition during periods of resource

scarcity. On the Masoala Peninsula of eastern Madagascar, co-occurring lemurs adapt their foraging behavior to variations in food availability, feeding jointly during the productive hot season but in spatial separation during the cold season (Vasey, 2000). Sympatric new world primates in Bolivia maintain long-term associations throughout the year by using different food resources when fruits are scarce (Porter, 2001). Also, habitat partitioning between competing haplorrhines in Kenya was observed to change with resource supply with one species shifting its foraging grounds during dry periods (Wahungu, 1998). Divergent habitat selection also stabilized coexistence in other small mammals (Aunapuu and Oksanen, 2003). Thus, there is evidence from various taxonomic assemblages that behavioral flexibility stabilizes competitive coexistence of ecologically similar species.

Finally, there are numerous examples of predators indirectly increasing species diversity in ecological communities (Wootton, 1994; Estes et al., 2011). Spatial segregation of resource competitors in relation to predation risk have been observed in many taxa (e.g., Paine, 1966; Hanski and Henttonen, 1996; Kullberg and Ekman, 2000; Rochette and Grand, 2004). Specific preference of intraguild predators for certain prey species are known from chimpanzees (Stanford, 1995; Teelen, 2007a,b, 2008), but the apparent preference of *M. coquereli* for *M. murinus* may rather be related to differences in the social organization between the mouse lemurs. In Finland, a more gregarious and abundant vole species prevailed over its sympatric congener in competition for space (Hughes et al., 2010) but was also more easily detectable and rewarding prey for predators (Norrdahl and Korpimäki, 1993; Koivisto et al., 2007).

CONCLUSION AND CONSERVATION IMPLICATIONS

This study extends the insights of previous single-site investigations of this cheirogaleid assemblage (Schwab and Ganzhorn, 2004; Dammhahn and Kappeler, 2008a,b) to a wider range of spatial scales, including the local scale, and links them to observed regional-scale patterns (Schäffler et al., 2015). To measure inter-specific interactions within transects, we developed an “Inter-Specific Index of Attraction” (ISIA) which we tested for statistical significance against a null model based on a combination of randomization and bootstrapping, which controls for intra-specific clustering.

The distribution of mouse lemurs indicated habitat partitioning at different levels. First, we detected a higher number of individuals in intact habitats during the wet season and in degraded habitat during the dry season. Our local scale analyses thus reconfirmed that both mouse lemur species crowded in most suitable forest areas during the wet season and tracked scarce resources in degraded habitats during the dry season, corresponding to the pattern described on the population-level (Schäffler et al., 2015). Interspecific competition between individuals within transects was indicated during the dry season predominately in non-degraded habitat, whereas spatial

segregation between *M. berthae* by *M. murinus* populations was limited to degraded habitat during the dry season (Schäffler et al., 2015). Increased use of degraded habitats when resources are scarce may therefore result from competitive exclusion between individuals in intact forests. Analyses incorporating dwarf and giant mouse lemurs with novel methods expanded knowledge on the interactions with third agents (Schäffler et al., 2015). The interspecific distribution of individuals confirmed that *C. medius* and *M. coquereli* mitigate competitive pressure on *M. berthae* and consequently stabilize mouse lemur coexistence. Our individual-level analyses revealed that the displacement of *M. murinus* by intraguild predator *M. coquereli* and the positive association between *M. berthae* and *M. coquereli* are not limited to non-degraded habitat during the dry season as previously suggested by the population-level distribution (Schäffler et al., 2015). Moreover, avoidance of superior competitor *C. medius* by *M. murinus* individuals and simultaneous local scale co-occurrence of *M. berthae* and *C. medius* during the wet season was not evidenced to date (Schwab and Ganzhorn, 2004; Schäffler et al., 2015). Given the variation in cheirogaleid distribution across spatio-temporal heterogeneities, the spatial competition hypothesis (Tilman, 1994) appears best suited to reconcile individual-level interspecific exclusion and population-level coexistence of the two mouse lemur species.

The complex ecological structure in the cheirogaleid assemblage of Menabe Central essentially depends on habitat quality and heterogeneity that provide cheirogaleids with refuges from unfavorable interspecific interactions and stabilizes competitive mouse lemur coexistence. *Microcebus berthae* was categorized as “Critically Endangered” in the recently updated IUCN Red List of Threatened Species (Markolf et al., 2020). Extensive habitat loss and degradation due to slash and burn agriculture results in continuing decline in the area of occupancy and extent of occurrence. A population decrease by more than 80% over 10 years is not only expected as a direct consequence of ongoing habitat loss, but also as interspecific interactions with dwarf and giant mouse lemurs that stabilize competitive coexistence of mouse lemurs depend on intact habitat. Contrasting association patterns of mouse lemurs between continuous forest sites (Rakotondravony and Radespiel, 2009) and isolated patches (Steffens and Lehman, 2016) in north-western Madagascar demonstrate the impact of habitat fragmentation on interaction regimes.

Species that are subject to the same disturbances do not always react in a similar manner, even if phylogenetically closely related (Lehman et al., 2006a,b,c; Irwin et al., 2010; Herrera et al., 2011; Lehman, 2016). It appears surprising that the massive landscape-level disturbances of recent times have not resulted in more lemur extinctions (Lehman et al., 2006c). However, species extinction in patchy environments may be time-delayed, and particularly threaten species that are abundant in intact habitat due to an interspecific trade-off between colonization and competitive abilities (Tilman et al., 1994). The loss of any species in ecological communities will have indirect effects on multiple levels (Strauss, 1991) and may trigger an extinction cascade with dramatic consequences for system stability (Allesina and Levine, 2011).

Genetic studies revealed that *M. coquereli* compensates for extensive population fluctuations (Kappeler, 2003) by

immigration from adjacent populations (Markolf et al., 2008). Continuing habitat fragmentation may permanently extirpate the species from forest patches if isolation prevents recolonization (Irwin et al., 2009). Metapopulation models for the eight species comprising a lemur assemblage in north-western Madagascar revealed differences in the ability to cope with habitat fragmentation: while the occurrence of all lemurs depended on patch size, *C. medius* was particularly susceptible to reduction of area and isolation of poorly connected habitat fragments (Steffens and Lehman, 2018). Further loss, degradation and fragmentation of dry forests in Menabe Central will likely cause a reduction of population size in *M. coquereli* and *C. medius* and release *M. murinus* from intraguild predation and resource competition. Increasing interspecific competition between the mouse lemurs would then further reduce the suitability of remaining habitat for *M. berthae*. In these scenarios, one mouse lemur species might drive the other one to extinction (Schwab and Ganzhorn, 2004). Protection of remaining intact forest parts as well as restoration of degraded habitat and connectivity in the central Menabe region of western Madagascar is therefore critical to preserve *M. berthae* and coexisting species in this global biodiversity hotspot.

NOTES ON THE STATISTICAL APPROACH

In this paper we tested interspecies associations involving mouse lemurs. Primarily, we were looking for negative associations that might be caused by competitive or (intraguild) predatory interactions. To do this we developed the “Inter-Species Index of Attraction” (ISIA) for local interactions on transects. We used a null model distinct from the ideal gas model because intraspecific clustering is in effect for all species and can obscure the effect of interspecies associations. To control for this, we used a null model based on a combination of randomization and bootstrapping to determine the significance of observed interactions. Our simulation approach comparing the neutral with the observed individual-level distribution of co-occurring species allowed for investigating interspecific interactions on a local scale and link it to observed regional scale patterns rather than examining only spatial overlap of populations (Schäffler et al., 2015). Moreover, our data collected from the cheirogaleid assemblage’s entire area of occupancy considered spatial heterogeneities and thus generated knowledge beyond the insights of previous studies at single sites (e.g. Schwab and Ganzhorn, 2004; Dammhahn and Kappeler, 2008a,b).

The statistical tests used by us in both regional and local analyses are non-parametric. One of the reasons for this is to avoid errors that might arise due to non-normality and zero-inflation in statistical tests. Another advantage of non-parametric statistics is that they are more robust against the effects of spatial autocorrelation. Some degree of spatial autocorrelation arising from external factors (Lennon, 2000) is likely to be present. One of the important external factors is habitat quality, which we controlled for by the fundamental structure of our data: dividing scenarios between degraded versus non-degraded. In comparisons between transect walks, the relatively large distances

between transects (>1 km) also reduces the effect of spatial autocorrelation. Another spatial issue arises from the fact that transect distribution was not strictly random, owing to the logistical difficulties of sampling a large number of transects in areas of dense forest.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the corresponding author upon request.

ETHICS STATEMENT

The animal study was reviewed and approved by Bundesamt für Naturschutz (BfN) in Germany; Ministère de l'Environnement et des Eaux et Forêts (MINEEF), CAFF/CORE committee and the National Association for the Management of Protected Areas (ANGAP) in Madagascar.

AUTHOR CONTRIBUTIONS

LS originally formulated the idea, developed the methodology, conducted fieldwork, and wrote the manuscript. PK provided the research facility and supported project implementation. LS and JH processed the data and performed analyses. JH developed the models and ran statistical analyses. All authors contributed to the article, approved the submitted version and agreed to be accountable for all aspects of the work.

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FUNDING

This study was completed with financial support from the German Primate Center (DPZ), Primate Conservation Incorporated (PCI Grant #359), Conservation International (CI), Durrell Wildlife Conservation Trust (DWCT) and with authorization by the CAFF/CORE committee, and the National Association for the Management of Protected Areas (ANGAP). Open access publication is kindly supported by the Zoological Research Museum Alexander Koenig (ZFMK).

ACKNOWLEDGMENTS

We thank Nielsen Rabarijaona, Rémy Ampataka, Raza Rakotonirina, Jean-Pierre Tolonjanahary, and Tiana Andrianjanahary for their expert assistance and outstanding commitment to the surveys, and Léonard Razafimanantsoa and Rodin Rasoloarison for logistic support during fieldwork. We also appreciate the suggestions of editor MB and the two reviewers DH and TS who helped to significantly improve our manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.585781/full#supplementary-material>

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- Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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