Received: 30 June 2023 | Revised: 28 September 2023 | Accepted: 20 October 2023

DOI: 10.1002/ajp.23572

RESEARCH ARTICLE

AMERICAN JOURNAL OF PRIMATOLOGY WILEY

Intergroup encounters in pair-living primates: Comparative analysis and a case study of pair-living and monogamous owl monkeys (*Aotus azarae*) of Argentina

Leonie Gussone[1,2] | **Alba García de la Chica**[3,4] | **Eduardo Fernandez-Duque**[4,5,6]

[1]Institute for Evolutionary Biology and Ecology, Bonn University, Bonn, Germany

[2]Department of Anthropology, University of Minnesota, Twin-Cities, Minnesota, USA

[3]Instituto de Ecología, Genética y Evolución, Universidad de Buenos Aires, Buenos Aires, Argentina

[4]Owl Monkey Project—Fundación ECO, Formosa, Argentina

[5]Department of Anthropology and School of the Environment, Yale University, New Haven, Connecticut, USA

[6]Facultad de Recursos Naturales, Universidad Nacional de Formosa, Formosa, Argentina

Correspondence

Leonie Gussone, Department of Anthropology, University of Minnesota, Twin-Cities, Minnesota, USA.
Email: gusso009@umn.edu

Funding information

National Geographic Society Education Foundation; Leakey Foundation; National Institutes of Aging; National Science Foundation; Wenner-Gren Foundation

Abstract

The function of intergroup encounters (IGEs) may differ substantially among species of different group sizes and social organizations. Research in group-living primates has shown that the behavioral responses during IGEs can vary widely from affiliative to neutral or aggressive interactions; still, little is known about IGEs in pair-living taxa. We conducted a systematic literature review to find relevant studies on the functions of IGEs in pair-living nonhuman primates that could inform analyses of IGE data ($n = 242$ IGEs, 21 groups and 10 solitary individuals, 1997–2020) from wild owl monkeys, a pair-living, monogamous primate with extensive biparental care. We identified 1315 studies published between 1965 and 2021; only 13 of them ($n = 10$ species) contained raw data on the number of IGEs. Our review of those studies showed that IGEs are common, but highly variable in their nature and characteristics in pair-living primates. To examine the non-mutually exclusive hypotheses of resource-, and mate defense, and infanticide avoidance we analyzed data from the Owl Monkey Project 27-year long database to build first an a priori model set. To incorporate prior knowledge from the literature review, we conducted our analyses as a consecutive series of binomial logistic regressions. All IGEs including all biologically relevant parameters ($N = 156$) were codified into three different behavioral categories (Reaction, Agonism, and Physical Aggression). The analysis showed that owl monkeys regularly engaged in IGEs, most of which were agonistic. They showed more reaction when infants were present, but reactions were less physically aggressive when infants and pregnant females were involved. Overall, our results lend more support for the infant and mate defense hypotheses than they do for the resource defense one.

KEYWORDS

between-group encounter, infanticide avoidance, mate-defense, pair-living, resource-defense

---

Abbreviations: AIC, Akaike Information Criteria; EDA, exploratory data analyses; IGE, intergroup encounter; I-T, information theoretic approach; OMP, Owl Monkey Project; PRISMA, preferred reporting items for systematic reviews and meta-analyses.

1 | INTRODUCTION

Between-group interactions are an important part of the social system of many animal species and are affected by the reproductive strategies of males and females, dispersal and intergroup spacing patterns, communication modalities, and population density (Boydston et al., 2001; Ferguson, 1988; Thompson et al., 2017; Van Belle, Grueter, et al., 2020). In primates, encounters between conspecific groups, or intergroup encounters (IGEs), are frequent in group-living species (Beehner & Kitchen, 2007; Christensen & Radford, 2018; Majolo et al., 2020). In these species, the behaviors during IGEs vary widely from affiliative interactions (black-tufted ear marmosets: Decanini & Macedo, 2008; Western gorillas: Bermejo, 2004; white-handed gibbons: Reichard & Sommer, 1997), to neutral encounters (Tana River crested mangabey: Kinnaird, 1992; Western gorillas: Bermejo, 2004; barbary macaques: Mehlman & Parkhill, 1988), to aggressive stand-offs (Tana River crested macaques: Kinnaird, 1992) and lethal attacks (chimpanzee: Boesch et al., 2008; Watts et al., 2006; crested macaques: Martinez Inigo, 2018).

This wide variation in the characteristics of IGEs as described in the literature may be due in part to different methodological practices and limitations. First, the presence of observers may produce a bias if not all members of neighboring groups are similarly habituated, even in study sites with projects spanning several years (Williamson & Feistner, 2003). Furthermore, a lack of standardization in definitions and terminology is likely to affect the reported frequency of IGEs. For example, depending on the study, IGEs are defined in terms of visual, physical, and/or vocal contact among groups or individuals (Fashing, 2001; Steenbeek, 1999; Van Belle, Porter, et al., 2020; Yi, Fichtel, Ham, et al., 2020). These potential sources of variation in the characteristics of IGEs can hamper cross-species and cross-population comparisons.

Over the years, most studies on interactions between primates' social groups have focused on intergroup agonism (Crofoot & Wrangham, 2010). Numerous factors have been suggested for promoting agonistic behaviors during IGEs, for example the presence of estrous females or the distribution of resources in space and time (Beehner & Kitchen, 2007; Fashing, 2001; Thompson et al., 2012). Furthermore, agonistic encounters are also substantially related to the species' ecological conditions and the selection pressures acting on both sexes (Beehner & Kitchen, 2007). Based on the expectation that female reproductive fitness is mainly determined by access to food resources (Trivers, 1972), it is expected that females will participate more frequently in IGEs when food resources are 'economically defendable'; in other words, when the benefits outcompete the costs and/or when food resources are at moderate abundance and occur primarily in discrete patches (Brown, 1964; Cheney et al., 1981; Ostfeld, 1990). Since the fitness of males is assumed to be mainly limited by access to reproductive females, their participation in agonistic IGEs has been related to the direct and indirect defense of their mates (Fashing, 2001; Wolf & Schulman, 1984) and infants (Fashing, 2001; van Schaik, 1996). If males are primarily defending their mates, then aggression will be mainly directed towards same-sex individuals (Beehner & Kitchen, 2007), when estrous females are present (Whitten et al., 2012), or when the female-male sex ratio or overall number of females is high (Beehner & Kitchen, 2007). If, on the other hand, the participation of males in intergroup aggression is mostly related to the defense of resources to attract females (Fashing, 2001), then males will show aggression towards both sexes when food is limited and defendable (Beehner & Kitchen, 2007; Kinnaird, 1992; Reichard & Sommer, 1997). Finally, because in some species unrelated adults try to kill infants of other groups during IGEs, males and females may also aim to defend infants and pregnant females from outgroup attacks (Koch et al., 2016).

Although the previously described hypotheses are not mutually exclusive (Beehner & Kitchen, 2007; Harris, 2007) most studies on IGEs only tested one of them, considering only certain variables and predictions in their analyses (e.g., Fashing, 2001; Garber et al., 1993). This may be problematic if it ignores processes potentially affecting IGEs because of the biases towards obvious patterns or preferred hypotheses (Betini et al., 2017). The relevance of any particular hypothesis is likely to differ between species and populations, and may be different for species with different social organizations and mating systems (Whitten et al., 2012). There is a long history in the scientific literature of recommending that multiple hypotheses be evaluated simultaneously to improve the process of scientific inference (Chamberlin, 1965; Dochtermann & Jenkins, 2011; Platt, 1968).

The different group structures characteristic of pair-living, uni-male/multi-female and multi-male/multi-females species illustrates the need to formalize hypotheses with attention to their species-specific biological relevance. In pair-living species, individuals are restricted by the number of conspecifics they can interact with, which, in turn, can lead to different fitness costs for individuals (Crofoot & Gilby, 2012). For example, pair-living males can sire a very limited number of offspring in any reproductive season when limiting their reproductive activities to one single female (Kappeler & Pozzi, 2019). This in turn makes the cost of extra-pair copulations comparatively high in these taxa (Brouwer & Griffith, 2019). Under these considerations, both the mate defense and infanticide avoidance hypotheses become especially relevant for explaining participation in IGEs. Furthermore, many pair-living species are territorial with individuals actively defending well-established home ranges that secure them access to resources critical for survival and reproduction (Tecot et al., 2016). In this context, males and females of territorial species may be also actively defending their food during IGEs.

The Azara's owl monkeys (*Aotus azarae*) from Formosa, Argentina, are pair-living, sexually and genetically monogamous primates that, in contrast to other species of the genus which are strictly nocturnal, show cathemeral activity patterns (Fernandez-Duque & de la Iglesia, 2023; Fernandez-Duque, Juárez et al., 2023; Fernandez-Duque, Rotundo, et al., 2023; Ziegler et al., 2022). In the Argentina population they are seasonal breeders producing a single infant once a year, usually born between late September and December (Corley et al., 2023; Fernandez-Duque et al., 2002). The species shows extensive levels of biparental care, with males carrying, grooming, and sharing food with infants more than females do (Fernandez-Duque et al., 2020; Garcia de la Chica et al., 2023; Huck & Fernandez-Duque, 2013). Azara's owl monkey groups are territorial, and, in Formosa, they actively defend their year-round stable home ranges that vary between 4 and 10 ha. When males and females become subadults they disperse from their natal groups and become solitary floater individuals (Corley & Fernandez-Duque, 2023; Corley, 2017; Fernandez-Duque, 2009; Huck & Fernandez-Duque, 2023). These floaters range without a fixed territory over the home ranges of established groups for a variable period and, in our population, we estimated the presence of two to five floaters for every 10 groups (Huck & Fernandez-Duque, 2017). While wandering as individual solitary floaters, these young adults try to gain breeding positions within established groups, something they accomplish by replacing same sex paired individuals. During 149 group-years, we registered 27 female and 23 male replacements from solitary floaters, suggestive of a similar competitive pressure for both sexes in the population (Fernandez-Duque & Huck, 2013).

In this population, between-group interactions are common, and they rarely involve serious fights. However, very aggressive, even lethal, encounters have been observed when solitary floaters were involved (Fernandez-Duque & Huck, 2013). Still, virtually nothing is known about solitary floaters in other pair-living primates. In species with such social organization, where it is likely that individuals live in groups with their relatives, individuals may be forced to disperse to reproduce. In red-bellied lemurs (*Eulemur rubriventer*), IGEs with solitary males occur, but at a lower rate than between breeding groups (Overdorff & Tecot, 2006). Solitary individuals move inconspicuously within the home range of breeding pairs and are chased away, aggressively, by both sexes. The inconspicuous lifestyle of solitary individuals and the fact that they are not often habituated and may react more strongly to the presence of human observers may be some of the reasons they have not been detected in more species (Fernandez-Duque et al., 2020; Huck & Fernandez-Duque, 2023). Further understanding of floaters could shed a different light on previously suggested hypotheses for the function of IGEs in pair-living species and should be therefore considered in the analyses of pair-living species social systems and sociality (Huck & Fernandez-Duque, 2023; Fernandez-Duque et al., 2020).

In this study, with the goal of identifying biologically relevant variables that had been associated with IGEs in pair-living primates, we first performed a systematic review of the literature. Then, to test predictions derived from the nonmutually exclusive hypotheses of resource-, and mate-defense, and infanticide avoidance (Table 1) we

TABLE 1 Hypotheses of intergroup encounters and predictions.

Hypotheses	Prediction and description
Resource defense H1: IGEs occur in response to groups competing for limited food resources.	Groups will react (behave actively in the presence of another group, see definition in Table 2) more during low food availability to secure nutrition. Bigger groups will react more during IGEs because they need more resources, especially during low food availability. Monkeys will react more when encounters occur at the core area of established territories since the core area is expected to contain the most food resources. The presence of pregnant females in groups will led to more reaction during encounters because pregnant females may require higher nutritional intake.
Mate defense H2: IGEs occur in response to groups defending their limited access to their mates.	IGEs will be more reactive if solitary individuals are involved because solitary individuals pose a threat to adults in groups by trying to gain their breeding positions. Because owl monkeys are seasonal breeders and there is only a short window for conception, individuals will be more reactive during IGEs happening in the mating season compared to the gestation and lactation season. IGEs will be less aggressive when pregnant females or infants are present because their presence in groups would indicate lower availability for mating opportunities. Since most subadult individuals become solitary floaters, IGEs will be more reactive when subadults close to the time of dispersal are involved, since they may use intergroup aggression to measure their chances for taking-over a breeding pair position.
Infanticide avoidance H3: IGEs occur in response to groups protecting their offspring from potential outgroup attacks.	IGEs will be more reactive when infants are present because parents could response more to defend them. IGEs will be less aggressive if infants are present, because newborn infants could be more vulnerable to injuries during aggressive IGEs.

examined the behavioral responses and environmental contexts of IGEs in wild Azara's owl monkeys (*Aotus azarae*).

2 | METHODS

2.1 | Systematic review

We conducted a systematic literature review (Paré et al., 2015; Xiao & Watson, 2019) to find articles and books reporting on IGEs in pair-living nonhuman primates. We used the database Web of Science (©Thomson Reuters Corporation) to filter the literature published between January 1965 and October 2021 for all studies containing any combination of search string of interest in the output's title, abstract or keyword (Figure 1).

We set the Web of Science Category to Behavioral Sciences only. Based on a priori criteria for inclusion we followed standardized procedures for Screening and Eligibility phases (Moher et al., 2009). We only included studies with a definition for intergroup encounter and raw data on the number of IGEs. The latter allowed us to calculate/evaluate at least one of the following measures for describing IGEs: frequencies of IGEs, frequency of aggressive ones, frequency of IGEs with solitary individuals or proportion of IGEs during the mating and the birth season or during high/low food availability. All other studies were considered irrelevant for our purposes. Additionally, we searched the bibliographies of all relevant studies for additional articles.

2.2 | IGEs in Azara's owl monkeys

The study site is located in the Province of Formosa, in northern Argentina (58°11′ W, 25°58′ S), and is part of the 1500 ha Reserva Privada Mirikiná, established in 2006. The area is part of the Gran Chaco region which contains a mosaic of grassland, savannahs, and dry and wet gallery forests (van der Heide et al., 2012). The weather is highly seasonal, characterized by marked fluctuations in rainfall, temperature, and photoperiod (Fernandez-Duque et al., 2002; Fernandez-Duque, 2016). Food availability also varies with seasons, and during the dry season (April to approx. August), mature edible fruits are relatively scarce in the forest (Fernandez-Duque, 2016; van der Heide et al., 2012). Birth seasonality is very marked in the area and consistent across years (Corley et al., 2023). In the area owl monkey groups actively defend their 4–10 ha home ranges. These home ranges have a core area that overlaps very little (11%) with other home ranges and a peripheral area with 48% overlap with other ranges (Wartmann et al., 2014).

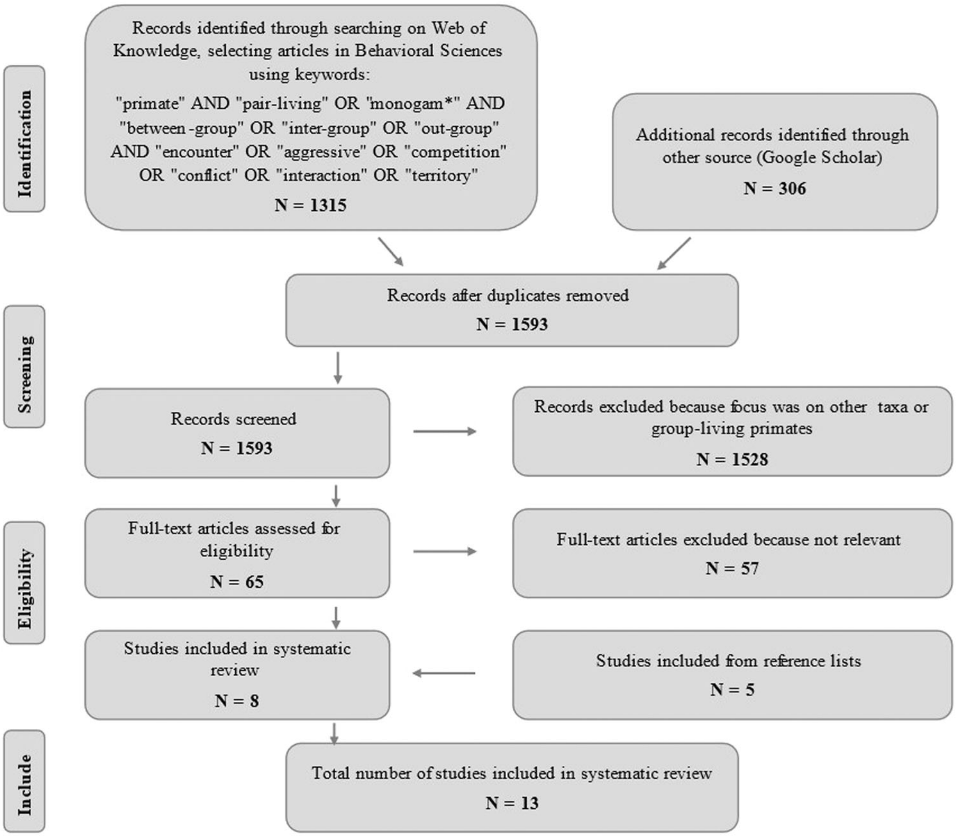

FIGURE 1 PRISMA (Preferred Reporting Items for Systematic reviews and Meta-Analyses) flow diagram (changed after Moher et al. (2009)) describing the steps taken, and the number of studies included/excluded at each step, to select the studies included in this literature review.

2.2.1 | Data collection

Every participant in the Owl Monkey Project (OMP) is trained so that every time a group of monkeys or a solitary individual is encountered, they enter an "avistaje" (i.e., a sighting) in a portable, electronic device which data is later exported to the OMP database. Entering an avistaje requires including records on demographic data, geolocation, and behaviors noted upon encounter. Then, if two groups/monkeys are seen at the same time by the same observer, two different avistajes will be recorded, one avistaje for each group. There is also a section for "notes", where observers can enter additional descriptive, complementary information. During training periods, the detailed and extended ethogram, and data collection protocol of the OMP are provided and explained to all observers. Observers are further pointed out to the social and sexual behaviors and contexts of particular interest, such as IGEs, mounts, vocalizations, aggressions, transfers of infants.

For the analyses we extracted all data used from avistajes in the Owl Monkey Project (OMP) relational Access database. For analyses, a sighting entry was identified as an IGE when the observer saw two groups or one group and one solitary individual at the same time (Table 2). For the analyses we used all data on IGEs recorded between 1997 and 2020.

We queried the OMP database to identify relevant IGEs data in the note's section of avistajes ($N = 16{,}904$). First, we searched for keywords related to IGEs in English or Spanish: "group," "grupo," "intergroup," "encounter," "encuentro," "solitary," "solitario," "enfrentamiento," "pelea," "fight," "corridas," "chasing." Given that field observations indicate that IGEs are often accompanied by vocalizations, we also searched avistajes for keywords related to owl monkey vocalizations: "turbinas," "turbine," "hoot," "graff," and "tonal." The identified relevant avistajes ($N = 5206$) were manually reviewed to identify IGEs between two groups, or one group and a solitary individual.

2.2.2 | Data analyses

The 242 IGEs we identified involved 21 groups (mean = 10.9 IGEs/per group; SD = 11; range = 1–34) and 10 solitary floater individuals (mean = 1.4 IGEs/individual; SD = 0.9; range = 1–4). Floaters participated in 37% (89/242) of all recorded IGEs; but they were the "focal" in only 6% (14/242) of IGEs. About two thirds of IGEs (156/242) had detailed descriptions to categorize the behavioral response of the group (Table 2) and data on the predictor variables (Table 3). In the analyzed IGEs, floaters participated in 36% (56/156)

TABLE 2 Behavioral response/categories during intergroup encounters and detailed description.

Category/behavioral response	Description
Intergroup encounter (IGE)	Two groups *or* one group and one solitary individual in visual proximity (observer can see both at the same time).
Reactive encounter	The involved monkeys behaved actively in the presence of the opposing group (e.g., approach, look in the direction, vocalize, chasing). Reactive encounters include agonistic and physically aggressive encounters.
Agonistic encounter	Interactions between groups involving vocalization, chasing, physical attacks. Agonistic encounters include physically aggressive encounters.
Physically aggressive encounter	Interactions between groups involving behaviors potentially causing injuries (e.g., bite, chasing, pushing).
Vocal encounter	The involved monkeys emitted sounds at each other, but no physical aggression was involved.

TABLE 3 Predictor variables, hypotheses and operational definitions used for analyses.

Predictor variable	Hypotheses	Operational definition for analyses
Season (categorical)	Food defense/mate defense	Mating/low food: April–August; Gestation/high food: August–November; Lactation/high food: December–March.
Area (categorical)	Food defense	Core/Periphery. When two groups met, the location was codified according to the focal group's home range. When a group encountered a solitary, the location was codified based on group's home range. NA when both groups were unknown, or for home ranges with no transect system (e.g., P300).
Group size (discrete numerical)	Food defense	# Individuals of all age classes.
Female pregnant (categorical)	Food defense/Mate defense	Yes/No female pregnant in at least one of the encountered groups (Gestation period ~120 day, counting back from birth).
Solitary present (categorical)	Mate defense/Infanticide avoidance	Yes/No solitary involved in IGE.
Subadult present (categorical)	Mate defense	Yes/No subadult close to dispersal present in at least one of the encountered groups (Close to dispersal: 120 day before dispersal event).
Infant present (categorical)	Infanticide avoidance	Yes/No infant present in at least one of the encountered groups (<6 months old).

and were the "focal group" in 4% (7/156). The OMP database provided information on group size and composition during IGEs, as well as on the rest of the variables of interest for analyses.

To inform our inferential statistical analyses, we first performed exploratory data analyses (EDA). The EDA did not reveal any strong associations among our predictor variables, so we included them all in subsequent analyses. Even when we predicted some interactions among variables to be biologically relevant (e.g. groups will react more aggressively towards solitary floater individuals during the mating season), we did not include those in our analyses to avoid model overfitting and subsequent model convergence problems and large inaccuracy of the parameter estimates given the relatively small number of observations (Garamszegi, 2016).

We took an Information-Theoretic approach (Burnham & Anderson, 2002) to select and compare generalized linear mixed models (Bolker et al., 2009). For model building we selected parameters considered to be biologically relevant for the characteristics of IGEs in other pair-living primates and mammals based on previous findings in other taxa and from our literature review (e.g. Bonadonna et al., 2017; Overdorff & Tecot, 2006; Reichard & Sommer, 1997).

We performed all statistical analyses in R version 4.0.3 (R Core Team, 2021). To incorporate prior knowledge, and given our research question and type of data, we conducted our analyses as a consecutive series of binomial logistic regressions (Cox & Snell, 1970) (Figure 2). Each IGE was classified for each of three nonmutually exclusive categories (Reaction, Agonism, and Physical Aggression) (Table 2).

We modeled our data in three different stages, evaluating the performance of our predictor variables in explaining each of the three behavioral outcomes. Stage 1 consisted of modeling the response variable Reaction using the complete data set of 156 IGEs to estimate the log-odds of individuals reacting during an IGE. During Stage 2, we completed the model-selection process using the subset of IGEs that excluded those individuals who did not show an observable reaction to compute the log-odds of individuals showing Agonism during an IGE. Finally, Stage 3 analyses allowed us to estimate the log-odds of Physical aggression during IGEs.

For all three stages we built a full model with binomial theoretical distribution that included all our variables of interest as fixed effects and analyzed the data using multi-model inference and model averaging (Burnham & Anderson, 2002; Symonds & Moussalli, 2011). Predictor variables in the full model included "Season," "Area," "Group size," "Female Pregnant," "Infant Present," "Subadult Present," and "Solitary Floater Present" (Table 3). The variable group size (mean ± SD: 3.01 ± 1.23; range: 1–7) was centered around its mean and standardized before running the model. We accounted for dependence among observations from the same group and year by including a random effect for focal group, the opposing group, and year.

Using the function *dredge* from "MuMIn" package (Barton, 2022) we created the list of models with every possible combination (subsets) of predictor variables. Within each of the model sets per outcome variable, we calculated corrected Akaike Information Criteria (AICc) recommended for relatively "small" number of observations (stage one: 156, stage two: 119, stage 3: 109) and utilized delta AICc and AICc weights to assess the plausibility of the candidate models (Burnham & Anderson, 2004). Before fitting models, we set a priori criteria for selecting the model(s) that we would use in making scientific (i.e. as opposed to mathematical/statistical) inferences (Hubbard et al., 2019). We considered there to be a single "best" approximating model only if it had an AICc weight of >0.9 (Burnham & Anderson, 2002). Still, even when one "best" model was supported, we considered all those with a delta AICc < 2 and report their results when making scientific inferences from our models. When there was not a single best approximating model, we

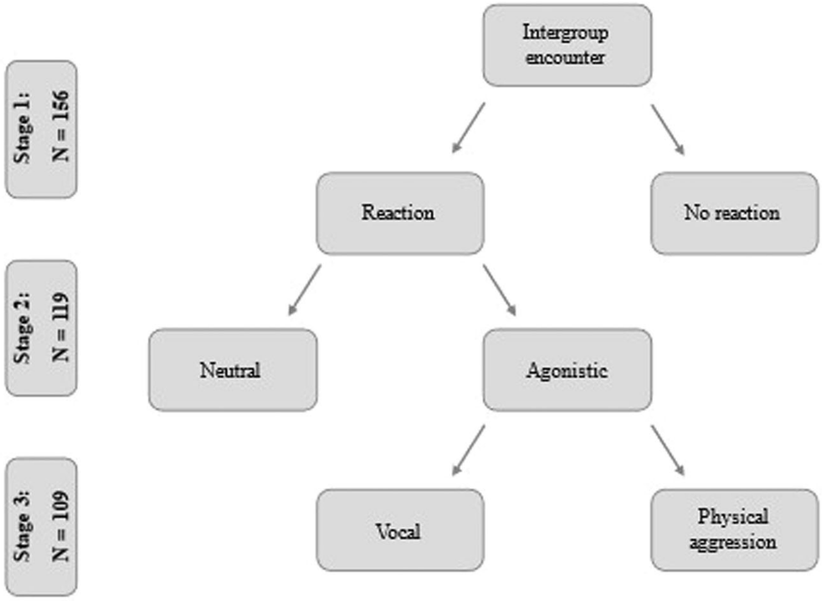

FIGURE 2 Flow-diagram of the three stages of our analysis as consecutive series of binomial logistic regressions.

made statistical inferences utilizing multiple models by calculating model-averaged parameters (Burnham & Anderson, 2004; Symonds & Moussalli, 2011). We used the "AICcmodavg" packages to calculate AICc and other model index, as well as model-averaged-parameter estimates (Mazerolle, 2020). As recommended, we report characteristics (number of parameters [K], AICc, delta AICc, likelihood, AICc weight, and log-likelihood) for all candidate models, so that readers can assess the plausibility of each of the candidate models for themselves (Supporting Information S1: 3, 4, 5, 6). For descriptive statistics, we report the mean ± standard deviation, unless otherwise specified. In summary, our analyses focused on comparing plausible a priori models, ranking models by weighing their relative value and importance, and averaging variable estimates from multiple models when more than one model had comparable levels of support. It would be counter to the goals of the I-T approach to discuss estimates of parameters in our models in terms of statistical significance based on arbitrary thresholds. It would be a mistake to "use AIC to rank candidate models and then test to see whether the best model ('alternative hypothesis') is significantly better than the second-best model (the null hypothesis)" (Burnham & Anderson, 2002, p. 83).; instead, we present odds ratios for the reader to quantitatively evaluate the strength of the results.

3 | RESULTS

3.1 | Characteristic of IGEs in pair-living primates

We identified 13 studies on IGEs from 10 pair-living primate species for analyses from the systematic literature research. Most of the studies were conducted on a relatively small number of focal groups (4 ± 3, range: 2–16) and with much variation in the observation time (297 ± 239 day, range: 26–643 day) which was reported in several different units (e.g., days and hours). Most of the studies recorded more aggressive encounters than nonaggressive ones ($N_{aggressive} = 554$, $N_{non-aggressive} = 221$), and only three reported data on sex participation and initiation (Table 4).

Observations of solitary floaters were rarely reported in the pair-living primates' literature. Since only Overdorff and Tecot (2006) reported observations of solitary individuals, information about the observation of solitaries and IGEs that included them was gathered via personal correspondence with the authors of the respective studies (Table 4). Most researchers ($N = 4/5$) stated that solitary individuals had been observed in their study population. One exception was the population of Peruvian coppery titi monkeys, where, given the social system of the species and the dispersal pattern of subadults, solitaries are expected, but have never been observed. IGEs between solitary individuals and groups have been noted in only four species (owl monkeys, red-bellied lemurs, white-handed gibbons, and indris). Overdorff and Tecot (2006) reported five IGEs between established groups and solitary floaters within a 1-year study period in red-bellied lemurs.

3.2 | IGEs in Azara's owl monkeys

The monkeys reacted in 76% of the 156 IGEs (119/156). Of these, 92% (109/119) were agonistic, and 63% (69/109) of the agonistic IGEs involved physical aggression (Figure 2).

3.2.1 | Probability of reaction: Stage 1 models

The IGE was categorized as reactive when individuals behaved actively in the presence of other groups or solitary floaters (e.g., approach, look in the direction, vocalize, chasing) (Table 2). They reacted when encountering another group more often during periods of gestation (89%, 24/27) than mating (73%, 64/88) or lactation (76%, 31/41). They also reacted more frequently during periods of high food availability than low food availability (83%, 55/67 vs. 72%, 64/89), and within the core area of their territory than the periphery (79%, 76/96 vs. 70%, 43/60). When a pregnant female was present in one of the interacting groups, they reacted in 80% of encounters (40/50); and in 73% of them (29/40) when infants were present. When a solitary floater, or subadult individual, was involved in the IGE, individuals reacted in 73% (41/56) and 74% (29/39) of the cases respectively.

In this first stage of the analyses, we modeled the probability of any reaction during IGEs. Since this is a very broad category of behavioral response, the process of model-selection indicated that 110 of the 128 models accounted for 99% of the cumulative weight, and seven of them had a Delta AIC < 2 (Table 5, full results in Supporting Information S1: 4).

The predictor variable "season" was included in five of the seven models that had a Delta AIC < 2 (M17, M25, M19, M18, and M49). The averaged model indicated that the odds ratio of a reaction during the gestation period was 3.3 and 2.2 times higher than during the mating season and the lactation period, respectively (Table 5). The probability of reaction was also slightly higher in the core area than in the periphery (1.1), and when a pregnant female was present (1.1, Table 5). On the other hand, the probabilities of a reaction were lower when an infant (1.2) was present and equal when a solitary was present (1) (Table 6).

3.2.2 | Probability of agonistic reaction: Stage 2 models

When owl monkeys reacted, most reactions were agonistic (92%, 109/119). These were more frequent in the mating period than the gestation (94%, 60/64 vs. 92%, 22/24) or lactation periods (87%, 27/31). They reacted more frequently with agonism during low food than high food availability periods (94%, 60/64 vs. 89%, 49/55). When a pregnant female was present in one of the groups, the monkeys reacted agonistically in all but one instance (97%, 33/34). Agonistic reactions were also more frequently associated with the presence of a solitary floater (83%, 34/41), or subadult (97%, 28/29).

TABLE 4 Information on intergroup encounters of 11 pair-living primate species from 13 studies identified through a systematic review of the literature and of Azara's owl monkeys (*Aotus azarae*) from the Owl Monkey Project database (shaded in gray).

Species	Obs time	N groups	N IGEs	Frequency	Duration (min)	N aggressive	N vocal	N neutral	N affiliative	N Male participation	N Female participation	N core	N periphery	N high food	N low food	Solitaries observed	Reference
Aotus azarae	11,382 day	G: 21, S: 10	242	0.021/day	-	98	50	58	0	-	-	90	103	123	152	Yes	This study
Avahi laniger	26 day	2	0	-	-	0	0	0	0	-	-	-	-	-	-	-	Norscia and Borgognini-Tarli (2008)
Callicebus personatus personatus	35 day	2	2	0.05/day	-	0	2	0	0	-	-	-	-	-	-	-	Price and Piedade (2001)
Eulemur rubriventer	1500 h	2	18	0.01/h	17.1 (2–55)	18	0	0	0	-	-	-	-	0.03/h	0.003/h	Yes	Overdorff and Tecot (2006)
Hylobates lar	475 day	3	274	0.52/day	70	126	82	-	-	-	-	-	-	-	-	Yes*	Reichard and Sommer (1997)
Hylobates lar	109 day	2	90	0.8/day	54 (4–263)	52	18	5	15	-	-	-	-	-	-	-	Bartlett (2003)
Hylobates moloch	581 day	3	234	0.49/day	80 (3–293)	168	46	-	0	-	-	-	-	-	-	Yes*	Yi, Fichtel, Ham, et al. (2020)
Hylobates moloch	306 day	3	129	0.42/day	84	74	-	-	-	74	9	-	-	-	-	Yes*	Yi, Fichtel, Kim, et al. (2020)
Indri indri	643 day	16	30	0.05/day	-	4	26	0	0	-	-	1	29	-	-	Yes*	Bonadonna et al. (2017)
Indri indri	396 day	3	12	0.03/day	-	1	11	0	0	-	-	9	3	-	-	Yes*	Bonadonna et al. (2020)
Lepilemur ruficaudatus	-	8	24 (MM), 95 (FM), 3 (FF)	0.5/d (M), 0.2/day (F)	-	23 (MM), 22 (FM), 1 (FF)	-	-	-	-	-	-	-	-	-	Yes*	Hilgartner et al. (2012)
Pithecia pithecia	103 day	3	50	0.46/day	-	49	-	0	0	50	2	-	-	-	-	-	Whitten et al. (2012)
Plecturocebus cupreus	2750.8 h	7	21	0.007/h	-	16	16	-	-	21	19	-	-	-	-	-	Dolotovskaya et al. (2020)
Plecturocebus discolor	211 day	3	29	0.137/day	-	-	-	-	-	-	-	-	-	-	-	-	Van Belle, Grueter, et al. (2020)

Abbreviations: Duration (min), mean duration and range of duration of IGEs; Female participation, Number of IGEs with identified participation of females; FF, female-female encounter; Frequency, frequency of IGEs per day or hour; G, group; Male participation, Number of IGEs with identified male participation; MM, male–male encounter; *N* affiliative, Number of affiliative encounters; *N* aggressive, Number of aggressive IGEs; N core, Number of IGEs within the core area of the focal groups home range; *N* groups, number of observed groups; *N* high food, Number of IGEs during season of high food availability; *N* IGEs, number of Intergroup encounters; *N* low food, Number of IGEs during season of low food availability; *N* neutral, Number of neutral encounters; *N* periphery, Number of IGEs in the periphery of the focal groups home range; *N* vocal, Number of IGEs involving vocalization; Obs time, Observation time; S, solitary; *, indicate that information includes personal observations by researchers who were contacted via email; Solitaries observed, Have solitary floaters been observed in the focal population (yes/no).

In this second stage of the analyses, we modeled the probability of agonistic behavior during an IGE. The model-selection process indicated that 78 of the 128 models accounted for 99% of the cumulative weight, and only two had a Delta AIC < 2. The first one included the variables group size and the presence of an infant, whereas the second one included those variables and the presence of a pregnant female (Table 7, full results in Supporting Information S1: 5).

The odd ratio of groups getting involved in aggressive IGEs when infants were present decreased by 0.07 but increased by 2.14 when pregnant females were present (Table 8). Regarding group size, in IGEs involving more individuals (larger groups) the monkeys were 5.1 times more likely to react aggressively than during IGEs between smaller groups (mean ± SD group size: 3.01 ± 1.23; range: 1–7) (Figure 3).

3.2.3 | Probability of physical aggression: Stage 3 model

Owl monkeys reacted more often with physical aggression than they did vocally (63% vs. 37%, $N = 69/109$ vs. 40/109). These physical aggressive encounters were more frequent during mating (65%, 39/60) and gestation periods (64%, 14/22) than during lactation (59%, 16/27). More specifically, vocal agonistic behaviors were more frequent during lactation (41%, 11/27) than gestation (36%, 8/22) and mating periods (35%, 21/60). They also showed more physical aggression during times of low than high food availability (66%, 40/61 vs. 61%, 30/49). Physical aggression was also higher when IGEs occurred in the core area than in the periphery of groups' territories (65%, 45/60 vs. 62%, 24/39).

In the presence of pregnant females, infants, and subadults, IGEs involved similar rates of vocal and physical aggression. The percentage of IGEs that involved physical aggression was 51% (20/39) when a pregnant female was present, 54% (13/24) when infants were present, and 50% (14/28) when subadults were present. It was the presence of solitary floaters that elicited most frequently physical reactions (68%, 23/34).

In this third stage of the analyses, we evaluated the probability that agonistic behavior involving physical aggression occurred during an IGE. The model selection process indicated that 100 of the 128 models accounted for 99% of the cumulative weight; two models had a Delta AIC < 2 and they all included the variables "female pregnant," "infant present," and "subadult present" (Table 9, full results in Supporting Information S1: 6).

The model-averaged parameters indicate that physically aggressive IGEs were 4.1 and 3.5 times more likely when no pregnant females or no dependent infants were present, respectively (Table 10). Additionally, IGEs were 1.1 times more likely to be physically aggressive when no pre-dispersing subadult was present (Table 10). Since the model selection process led to one candidate model containing all three variables (M75), we

TABLE 6 Stage 1: Summary of model-averaged parameters.

Variable	Estimate	Std. Error	Lower CI	Upper CI	z Value
Intercept	2.25	0.87	0.52	3.98	2.55
Sc Period (Lactancy)	−0.78	0.80	−2.55	0.50	0.97
Sc Period (Mating)	−1.19	0.95	−3.09	−0.04	1.25
Location (Periphery)	−0.11	0.28	−1.19	0.40	0.39
Female pregnant Year	0.06	0.25	−0.49	1.56	0.79
Infant present Year	−0.14	0.37	−1.71	0.42	0.69
Solitary present Year	−0.03	0.15	−1.13	0.55	0.87

Note: All models with a delta AICc < 2 (M17, M1, M25, M19, M18, M49, and M2) were used to calculate model averaged estimates. Reference levels: Season = Gestation, Location = Core, Female pregnant = No, Infant present = No, Solitary present = No. Table shows estimates (coefficients), Std. Error (standard error for the estimate of the fixed effect), lower and upper bounds of the 95% confidence interval (CI) and *z*-value (the test statistic).

TABLE 5 Stage 1: a priori candidate models ranked by their corrected Akaike Information Criteria (AICc) values.

	K	AICc	Delta_AICc	AICcWt	LL
Mod17 Period + (1|Focal group) + (1| Second group) + (1|Year)	6	176.6	0.00	0.06	−82.03
Mod01 (1|Focal group) + (1| Second group) + (1|Year)	4	177.3	0.64	0.04	−84.50
Mod25 Infant present + Period + (1|Focal group) + (1| Second group) + (1|Year)	7	177.4	0.79	0.04	−81.33
Mod19 Female pregnant + Period + (1|Focal group) + (1| Second group) + (1|Year)	7	177.8	1.13	0.04	−81.49
Mod18 Area + Period + (1|Focal group) + (1| Second group) + (1|Year)	7	177.9	1.26	0.03	−81.56
Mod49 Period + Solitary present + (1|Focal group) + (1| Second group) + (1|Year)	7	178.4	1.75	0.03	−81.81
Mod02 Area + (1|Focal group) + (1| Second group) + (1|Year)	5	178.5	1.90	0.02	−84.06

Note: All models with delta AICc < 2 are reported.

TABLE 7 Stage 2: a priori candidate models ranked by their corrected Akaike Information Criteria (AICc) values. All models with delta AICc < 2 are reported.

	K	AICc	Delta_AICc	AICcWt	LL
Mod13 Group size + Infant present + (1 | Focal_group) + (1 | Group2) + (1 | Year)	6	66.8	0.00	0.72	−27.01
Mod15 Female pregnant + Group size + Infant present + (1 | Focal_group) + (1 | Group2) + (1 | Year)	7	68.6	1.84	0.29	−26.80

TABLE 8 Stage 2: Summary of model-averaged parameters.

Variable	Estimate	Std. Error	Lower CI	Upper CI	*z* Value
Intercept	4.39	1.34	1.73	7.05	3.24
Group size	1.63	0.67	0.29	2.97	2.39
Infant present Year	−2.67	1.14	−4.93	−0.40	2.31
Female pregnant Year	0.22	0.73	−1.65	3.16	0.77

Note: All models with a delta AICc < 2 (M13, M15) were used to calculate model averaged estimates. Reference levels: Group Size = mean, Female pregnant = No, Infant present = No. Table shows estimates (coefficients), Std. Error (standard error for the estimate of the fixed effect), lower and upper bounds of the 95% confidence interval (CI), and *z* Value (the test statistic).

show graphically the estimated values of all parameters of interest (Figure 4).

4 | DISCUSSION

4.1 | Literature review

We systematically reviewed 13 studies (10 species) on IGEs in pair-living primates. The literature review showed that these encounters are common, but highly variable in their characteristics in species with this type of social organization. We hypothesized that a major cause of this variation may be due to differences in the methodological approach and posterior analyses, which, in consequence, also hampers possible comparisons. For example, Yi, Fichtel, Ham, et al. (2020) defined an intergroup encounter in Javan gibbons to occur when two different groups were within 50 m of each other. In stark contrast, Dolotovskaya et al. (2020) recorded an intergroup encounter in coppery titi monkeys if individuals of the study groups had visual contact with another group and responded to its presence by calling and/or chasing. With the latter definition, all neutral between-group encounters, those with no or little interaction, were excluded, thereby lowering the frequency of recorded encounters. This type of definition may explain why most studies reported more aggressive encounters between groups than nonaggressive encounters in pair-living primates (Bonadonna et al., 2017; Dolotovskaya et al., 2020; Hilgartner et al., 2012). Furthermore, every reviewed study focused on different aspects of IGEs. For example, one study reported frequencies of IGEs for seasons of high and low food availability (Overdorff & Tecot, 2006), a second one the different amounts of IGEs within the core area and the periphery of the focal group's home range (Bonadonna et al., 2020), and two other ones reported sex differences in participation and initiation during IGEs (Dolotovskaya et al., 2020; Whitten et al., 2012). Given that the proposed hypotheses (mate-, and resource defense, and infanticide avoidance) are not mutually exclusive, future studies should be designed to include multiple variables that will allow the testing of simultaneous predictions derived from different hypotheses (Harris, 2007).

The number of studied groups and the observation time also varied greatly among studies (Groups range: 2–22; Time range: 26–11,382 day). Accordingly, the frequency of IGEs was highly variable, ranging from 0.02 per day in owl monkeys (this study), to 0.8 per day in white-handed gibbons (Bartlett, 2003). It must be noted that IGEs may have species-specific or even population-specific functions, and the variation in results may also be related to species-specific ecological and/or behavioral dynamics. For example, in one population of group-living bonnet macaques (*Macaca radiata*), IGEs occurred at a rate of 1.4 encounters/day, while in a second population of the same species the same authors only registered 0.77 encounters/day (Cooper et al., 2004). The authors suggested that differences in population densities, distribution of resources, and territories overlap between the two study populations would explain the variation found. In pair-living primates, the overlap among territories is highly variable (e.g., white handed gibbons: 17% Yi, Fichtel, Kim, et al., 2020; red-bellied lemurs: 8% Overdorff & Tecot, 2006; indris: 1−3% Bonadonna et al., 2017), and population densities have not been properly explored yet.

Most authors we contacted of the studies in our review reported having observed solitary floaters in their study populations. Yet, these individuals were not usually considered in density surveys or mentioned in published studies. Among primates, it is only in the owl monkey population of Argentina that a substantial floater population has been documented and studied systematically since 2002 (Corley, 2017; Fernandez-Duque & Huck, 2013; Garcia de la Chica et al., 2021; Huck & Fernandez-Duque, 2017, 2023). Given that the presence of solitary floaters seems to be related to the rate of encounters, and that interactions with floaters may have profound consequences for reproductive pairs (Fernandez-Duque & Huck, 2013), we strongly recommend that researchers systematically report in all studies whether or not solitary floaters are present in the study population. It is important that this information be included in studies depicting the species' natural history as well as in more theoretical work on population dynamics and the evolution of social

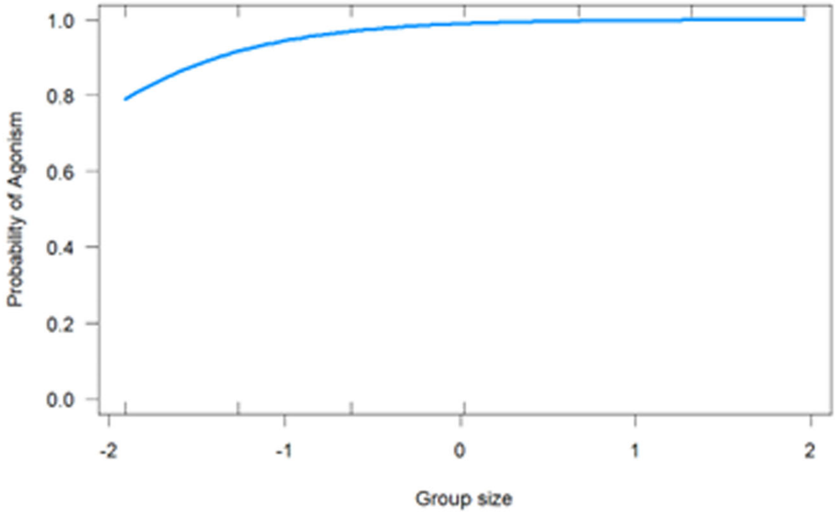

FIGURE 3 Probability of agonistic behavior during an IGE in relation to the focal group's group size (mean ± SD: 3.09 ± 1.23) Group size is z-transformed.

TABLE 9 Stage 3: A priori candidate models ranked by their corrected Akaike Information Criteria (AICc) values.

	K	AICc	Delta_AICc	AICcWt	LL
Mod11 Female pregnant + Infant present + (1 | Focal_group) + (1 | Group2) + (1 | Year)	6	139.8	0.00	0.67	−63.47
Mod75 Female pregnant + Infant present + Subadult present + (1 | Focal_group) + (1 | Group2) + (1 | Year)	7	141.2	1.47	0.32	−63.06

Note: All models with delta AICc < 2 are reported.

TABLE 10 Stage 3: Summary of model-averaged parameters.

Variable	Estimate	Std. Error	Lower CI	Upper CI	*z* Value
Intercept	1.63	0.61	0.42	2.84	2.65
Female pregnant Year	−1.45	0.66	−2.75	−0.14	2.17
Infant present Year	−1.29	0.65	−2.58	0.00	1.96
Subadult present Year	−0.19	0.47	−1.90	0.72	0.41

Note: All models with a delta AICc < 2 (M11 and M75) were used to calculate model averaged estimates. Reference levels: Female pregnant = No, Infant present = No, Subadult present = No. Table shows estimates (coefficients), Std. Error (standard error for the estimate of the fixed effect), lower and upper bounds of the 95% confidence interval (CI), and *z* Value (the test statistic).

systems in primates (Fernandez-Duque et al., 2020; Huck & Fernandez-Duque, 2023; Huck et al., 2020).

Additionally, sex-differences in participation and initiation of IGEs are particularly difficult to assess in arboreal species with inconspicuous (to the observer) sexual dimorphism in size and/or coloration, such is the case in many pair-living primates (Gamba et al., 2016; Huck et al., 2011). Besides this, in the case of cathemeral and nocturnal owl monkeys (*Aotus* spp.) (Fernandez-Duque et al., 2010; Link et al., 2023) their activity patterns make it even more difficult to properly assess the sex of participants when they are not identifiable by means of tags or collars (Fernandez-Duque, Juárez et al., 2023; Fernandez-Duque, Rotundo, et al., 2023).

Undoubtedly, information on the age and sex of individuals participating in IGEs is critical for testing more specific predictions derived from the hypotheses proposed. In fact, given that IGEs may be particularly risky for species where the cost of extra-pair copulations is higher, as expected for pair-living primate species, observational and genetic evaluations of the actual mating systems of the species (i.e., rates of extra-pair paternity) are needed to unravel male and female reproductive strategies. This would help us to further elucidate the function of mate defense and infanticide avoidance behaviors in these species, including owl monkeys. A valuable tool that can contribute to addressing these questions are field experiments, such as playback experiments, which can allow us to evaluate male and female behavioral responses to simulated groups or solitary floaters in wild populations (Caselli et al., 2015; Dolotovskaya & Heymann, 2022; Garcia de la Chica et al., 2021).

4.2 | IGEs in pair-living owl monkeys

The analysis of IGEs from the Owl Monkey Project data set showed that owl monkeys regularly engaged in IGEs, most of which included agonistic behavior. Our results lend more support to the mate

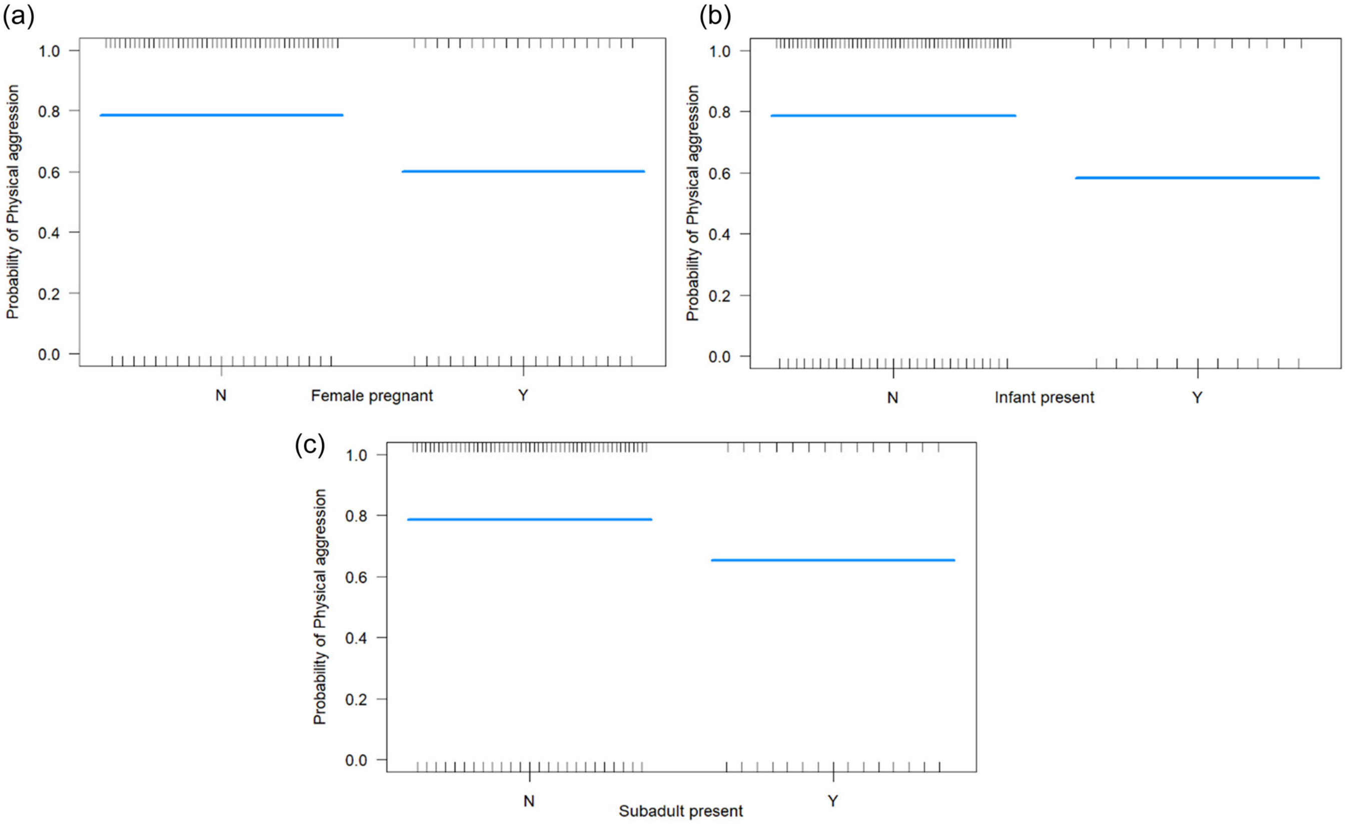

FIGURE 4 Probability of involvement of physical aggression during an IGE (a) when a pregnant female was present (b) when an infant was present (c) when a subadult individual close to dispersal was present. Black tick marks show the number of IGEs including physical aggression (1.0) or not including physical aggression (0.0) for each variable, e.g. when no pregnant female was present 41 IGEs were aggressive (top left tick marks) and 21 IGES were not aggressive (bottom left tick marks).

defense and the infanticide avoidance hypotheses than they do to the resource defense hypothesis The evidence was inconclusive on which factors initiated an observable reaction when two groups encountered each other. However, when behavioral responses were analyzed following more detailed criteria (i.e., Agonism [Stage 2] and Physical Aggression [Stage 3]), results showed that groups were more likely to react agonistically when the focal group was larger and pregnant females were involved. When infants and pregnant females were present the encounters were less likely to include physical aggression. This indicates that the groups limited their agonistic behaviors to vocal displays instead of physical fights when pregnant females were involved. Together, these results suggest that groups may avoid aggressive encounters when carrying dependent infants, supporting the infanticide avoidance hypothesis. Infanticide has not been observed in *A. azarae*, nor in sakis, or titis (Fernandez-Duque et al., 2020). Since owl monkeys show extensive biparental care (Fernandez-Duque et al., 2020; Garcia de la Chica et al., 2023; Huck & Fernandez-Duque, 2013), both males and females should aim to protect their infants. The replacement of males is associated with a reduction of offspring survival (Garcia de la Chica et al., 2023); therefore, mate defense might be important to guarantee the survival of infants. Nevertheless, as previously stated, future studies on the species should aim to get better quality data on the sex of participants and initiators of encounters to better evaluate these hypotheses. For example, to avoid infanticide, pregnant or nursing females could react more agonistically towards potentially infanticidal intruders by using vocalizations (Rosenbaum et al., 2016). On the other hand, because females need more resources to sustain pregnancy and early infant development (Clutton-Brock, 2007), females may react more towards other groups during pregnancy to ensure access to necessary resources while avoiding fights that can endanger the pregnancy. Accordingly, although in our study we did not find strong evidence for the type of period (i.e., mating, gestation, and lactation) being a predictor of agonistic reactions or aggressive fights, future studies should analyze the reproductive cycle of females involved in IGEs in more detail. To that end, hormonal data and behavioral observations should be used to determine if females are cycling. If cycling receptive females are present in the group, then males may react more aggressively towards intruding males. Nonetheless, it is important to note that sexual selection may act similarly for males and females in owl monkeys (Garcia de la Chica et al., 2021; Huck et al., 2020; Spence-Aizenberg et al., 2018), therefore, mate defense behaviors would be expected in both sexes, and should not only be analyzed in males.

Regarding the presence of pre-dispersing subadults, IGEs were less likely to be physically aggressive when these individuals were involved. In other primate species, although subadult individuals may initiate between-group encounters to gain information about potential breeding positions, or to practice for future territory or mate defense, IGEs may be less physically aggressive since non-reproductive individuals do not represent a direct threat to mated individuals (Japanese macaques: Majolo et al., 2005; white-faced sakis: Whitten et al., 2012)

Contradicting the predictions derived from the resource defense hypothesis, owl monkeys were more likely to react during high food availability (Korstjens et al., 2005; Reichard & Sommer, 1997). Still, when food was abundant, the location of the encounter and the season did not predict the probability of a reaction to be agonistic or to involve physical aggression. Since participation in IGEs is costly, groups may react more when more resources are available, and individuals are in better physical condition. In other words, when resources are scarce, the potential costs of tolerating other groups in the core area could likely be higher. On the other hand, when food availability is high, food may be abundant enough that between-group encounters can be resolved more often without agonistic interactions. A similar pattern has been reported in pair-living red-bellied lemurs; IGEs occurred more frequently with the sympatric rufous lemurs during high food availability, while they defended their feeding sites more aggressively during low food availability (Overdorff & Tecot, 2006). The authors suggested that finding alternative food sources may exceed the costs of defending the feeding site when food availability is low. Javan gibbons show similar patterns; males participated more often in IGEs when food availability was high, suggesting that competing over limited resources may be too costly for them (Yi, Fichtel, Ham, et al. (2020). In agreement with this, we found that the probability of an agonistic reaction was higher with increasing group sizes, which may be explained by the higher nutritional requirements of larger groups. Nevertheless, it must be noted that, in our analysis, food availability was only categorically estimated as dry and wet season. Even when this preliminary classification may give us a first hint of ongoing patterns of resource defense, a better description of the abundance and quality of resources within the groups' home ranges, as well as site feeding intensity, is needed to enable more accurate predictions derived from the food defense hypothesis (Brown, 2013).

IGEs occur infrequently and are difficult to observe (Harris, 2007). Thus, the observation of IGEs may be biased towards agonistic and aggressive encounters because these usually include loud vocalizations. This may contribute to the inconclusive findings in the first stage of our analysis. It can be expected that IGEs without any reaction occurred more frequently than we recorded. Furthermore, especially in the cathemeral owl monkeys (Fernandez-Duque et al., 2001), IGEs may frequently happen during the night, which leads to an additional underestimation of the number of encounters.

In conclusion, our study provides evidence that the function and characteristics of IGEs are highly variable in pair-living primates. The analysis of multiyear data on wild owl monkeys contributes to the understanding of the mechanisms of IGEs and the behavioral responses in pair-living primates in general, and in owl monkeys specifically. Furthermore, our research provides important information about the influence of solitary floaters on the behavioral responses of groups during encounters emphasizing the importance to include floaters in future studies of between-group interactions in all pair-living species.

AUTHOR CONTRIBUTIONS

Leonie Gussone: Conceptualization (supporting); formal analysis (lead); investigation (lead); methodology (lead); visualization (lead); writing—original draft (lead); writing—review and editing (equal). **Alba García de la Chica**: Conceptualization (equal); data curation (equal); formal analysis (supporting); investigation (supporting); methodology (supporting); project administration (equal); supervision (equal); validation (equal); writing—original draft (supporting); writing—review and editing (equal). **Eduardo Fernandez-Duque**: Conceptualization (lead); data curation (lead); formal analysis (supporting); funding acquisition (lead); investigation (supporting); methodology (supporting); project administration (lead); supervision (lead); validation (supporting); writing—original draft (supporting); writing—review and editing (supporting).

ACKNOWLEDGMENTS

Fieldwork for this project was supported through grants to EFD from the Wenner-Gren Foundation, the L.S.B. Leakey Foundation, the National Geographic Society, the National Science Foundation (NSF-BCS-0621020, 1232349, 1503753, 1848954; RAPID-1219368, DDIG-1540255; NSF-REU 0837921, 0924352, and 1026991) and the National Institutes of Aging (to EFD), NIA- P30 AG012836-19, NICHD R24 HD-044964-11, as well as institutional and logistical support from San Diego Zoo Global (formerly the Zoological Society of San Diego), the University of Pennsylvania and Yale University. We want to thank Dr. Ulrich Reichard, Dr. Stacey Tecot, Dr. Sofya Dolotovskaya, and Dr. Yoonjung Yi for the interesting and insightful conversations about solitary floaters in other pair-living primates and Review Editor M. Norconk and two anonymous reviewers for comments that helped us improve the manuscript. Research by the OMP has been approved by the University of Pennsylvania, Yale University, the Formosa Province Council of Veterinarian Doctors, the Directorate of Wildlife, the Subsecretary of Ecology and Natural Resources and the Ministry of Production. We thank Bellamar Estancias and Fundación E.C.O. for the continued support of the OMP and all the researchers who assisted in the field. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data for all analyses reported in this study is available upon request to the authors.

ORCID

Leonie Gussone http://orcid.org/0000-0001-9996-6339

REFERENCES

Bartlett, T. Q. (2003). Intragroup and intergroup social interactions in White-handed gibbons. *International Journal of Primatology*, *24*, 239–259. https://doi.org/10.1023/A:1023088814263

Barton, K. (2022). Package 'MuMIn' Version 1.46.0, *R PackageVersion 1.46.0*.

Beehner, J., & Kitchen, D. (2007). Factors affecting individual participation in group-level aggression among non-human primates. *Behaviour*, *144*(12), 1551–1581. https://doi.org/10.1163/156853907782512074

Van Belle, S., Grueter, C. C., & Furuichi, T. (2020). Dynamics of intergroup relationships in primates: Introduction to the special issue. *International Journal of Primatology*, *41*, 163–170. https://doi.org/10.1007/s10764-020-00159-2

Van Belle, S., Porter, A. M., Fernandez-Duque, E., & Di Fiore, A. (2020). Ranging behavior and the potential for territoriality in pair-living titi monkeys (*Plecturocebus discolor*). *American Journal of Primatology*, *83*(5), e23225. https://doi.org/10.1002/ajp.23225

Bermejo, M. (2004). Home-Range use and intergroup encounters in Western gorillas (*Gorilla g. gorilla*) at lossi forest, north Congo. *American Journal of Primatology*, *64*(2), 223–232. https://doi.org/10.1002/ajp.20073

Betini, G. S., Avgar, T., & Fryxell, J. M. (2017). Why are we not evaluating multiple competing hypotheses in ecology and evolution? *Royal Society Open Science*, *4*(1), 160756. https://doi.org/10.1098/rsos.160756

Boesch, C., Crockford, C., Herbinger, I., Wittig, R., Moebius, Y., & Normand, E. (2008). Intergroup conflicts among chimpanzees in taı national park: Lethal violence and the female perspective. *American Journal of Primatology*, *70*(6), 519–532. https://doi.org/10.1002/ajp.20524

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H., & White, J. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Bonadonna, G., Torti, V., Sorrentino, V., Randrianarison, R. M., Zaccagno, M., Gamba, M., Tan, C. L., & Giacoma, C. (2017). Territory exclusivity and intergroup encounters in the indris (*Mammalia: Primates: Indridae: Indri indri*) upon methodological tuning. *The European Zoological Journal*, *84*(1), 238–251. https://doi.org/10.1080/24750263.2017.1318184

Bonadonna, G., Zaccagno, M., Torti, V., Valente, D., De Gregorio, C., Randrianarison, R. M., Tan, C., Gamba, M., & Giacoma, C. (2020). Intra- and intergroup spatial dynamics of a Pair-Living singing primate, *Indri indri*: A multiannual study of three indri groups in maromizaha forest, Madagascar. *International Journal of Primatology*, *41*(2), 224–245. https://doi.org/10.1007/s10764-019-00127-5

Boydston, E. E., Morelli, T. L., & Holekamp, K. E. (2001). Sex differences in territorial behavior exhibited by the spotted hyena (*Hyaenidae, Crocuta crocuta*). *Ethology*, *107*(5), 369–385. https://doi.org/10.1046/j.1439-0310.2001.00672.x

Brouwer, L., & Griffith, S. C. (2019). Extra-pair paternity in birds. *Molecular Ecology*, *28*(22), 4864–4882. https://doi.org/10.1111/mec.15259

Brown, J. L. (1964). *The Evolution of Diversity in Avian Territorial Systems* (pp. 160–169).

Brown, M. (2013). Food and range defence in group-living primates. *Animal Behaviour*, *85*(4), 807–816. https://doi.org/10.1016/j.anbehav.2013.01.027

Burnham, K., & Anderson, D. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). Springer New York LLC.

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference understanding AIC and BIC in model selection. *Socioecological Methods & Research*, *33*(2), 261–304. https://doi.org/10.1177/0049124104268644

Caselli, C. B., Mennill, D. J., Gestich, C. C., Setz, E. Z., & Bicca-Marques, J. C. (2015). Playback responses of socially monogamous black-fronted titi monkeys to simulated solitary and paired intruders. *American Journal of Primatology*, *77*(11), 1135–1142.

Chamberlin, T. C. (1965). The method of multiple working hypotheses. *Science*, *148*(3671), 754–759. https://doi.org/10.1126/science.148.3671.754

Cheney, D. L., Lee, P. C., & Seyfarth, R. M. (1981). Behavioral correlates of Non-Random mortality among Free-Ranging female vervet monkeys. *Behavioral Ecology and Sociobiology*, *9*(2), 153–161. https://doi.org/10.1007/BF00293587

Christensen, C., & Radford, A. N. (2018). Dear enemies or nasty neighbors? causes and consequences of variation in the responses of group-living species to territorial intrusions. *Behavioral Ecology*, *29*(5), 1004–1013. https://doi.org/10.1093/beheco/ary010

Clutton-Brock, T. (2007). Sexual selection in males and females. *Science*, *318*(5858), 1882–1885. https://doi.org/10.1126/science.1133311

Cooper, M., Aureli, F., & Singh, M. (2004). Between-group encounters among bonnet macaques (*Macaca radiata*). *Behavioral Ecology and Sociobiology*, *56*, 217–227. https://doi.org/10.1007/s00265-004-0779-4

Corley, M., & Fernandez-Duque, E. (2023). Dispersal: A Critical Life History Stage Influencing Populations, Social Dynamics, and Individual Fitness. *Owl monkeys: Biology, adaptive radiation, and behavioral ecology of the only nocturnal primate in the Americas* (pp. 423–459). Springer International Publishing. https://doi.org/10.1007/978-3-031-13555-2_15

Corley, M., Spence-Aizenberg, A., Fernandez-Duque, E., & Valeggia, C. (2023). Reproductive ecology and behavioral endocrinology of owl monkeys. *Owl monkeys: Biology, adaptive radiation, and behavioral ecology of the only nocturnal primate in the Americas* (pp. 265–300). Springer International Publishing. https://doi.org/10.1007/978-3-031-13555-2_9

Corley, M. K. (2017). *Leaving home: Demographic, endocrine, and behavioral correlates of dispersal in monogamous owl monkeys* (Aotus azarae) *of argentina*. University of Pennsylvania.

Cox, D. R., & Snell, E. J. (1970). *Analysis of binary data* (2nd ed.). Routledge. https://doi.org/10.1201/9781315137391

Crofoot, M. C., & Gilby, I. C. (2012). Cheating monkeys undermine group strength in enemy territory. *Proceedings of the National Academy of Sciences*, *109*(2), 501–505. https://doi.org/10.1073/pnas.1115937109

Crofoot, M. C., & Wrangham, R. W. (2010). Intergroup aggression in primates and humans: The case for a unified theory. *Mind the gap: Tracing the origins of human universals* (pp. 1–503). Springer. https://doi.org/10.1007/978-3-642-02725-3

Decanini, D. P., & Macedo, R. H. (2008). Sociality in *Callithrix penicillata*: II. individual strategies during intergroup encounters. *International Journal of Primatology*, *29*, 627–639. https://doi.org/10.1007/s10764-008-9265-6

Dochtermann, N. A., & Jenkins, S. H. (2011). Developing multiple hypotheses in behavioral ecology. *Behavioral Ecology and Sociobiology*, *65*(1), 37–45. https://doi.org/10.1007/s00265-010-1039-4

Dolotovskaya, S., & Heymann, E. W. (2022). Coordinated singing in coppery titi monkeys (Plecturocebus cupreus): Resource or mate defense? *Frontiers in Ecology and Evolution*, *10*, 898509.

Dolotovskaya, S., Walker, S., & Heymann, E. W. (2020). What makes a pair bond in a neotropical primate: Female and male contributions. *Royal Society Open Science*, *7*(1), 191489. https://doi.org/10.1098/rsos.191489

Fashing, P. (2001). Male and female strategies during intergroup encounters in guerezas (*Colobus guereza*): Evidence for resource defense mediated through males and a comparison with other primates. *Behavioral Ecology and Sociobiology*, *50*(3), 219–230. https://doi.org/10.1007/s002650100358

Ferguson, J. W. H. (1988). Comparison of communication and signalling patterns of whitebrowed sparrowweavers and other gregarious ploceid weavers. *Ostrich*, *59*(2), 54–62. https://doi.org/10.1080/00306525.1988.9633696

Fernandez-Duque, E. (2009). Natal dispersal in monogamous owl monkeys (*Aotus azarai*) of the argentinean chaco. *Behaviour*, *146*(4), 583–606. https://doi.org/10.1163/156853908X3979

Fernandez-Duque, E. (2016). Social monogamy in wild owl monkeys (*Aotus azarae*) of Argentina: The potential influences of resource distribution and ranging patterns. *American Journal of Primatology*, *78*(3), 355–371. https://doi.org/10.1002/ajp.22397

Fernandez-Duque, E., & Huck, M. (2013). Till death (Or an Intruder) do us part: Intrasexual-Competition in a monogamous primate. *PLoS One*, *8*(1), e53724. https://doi.org/10.1371/journal.pone.0053724

Fernandez-Duque, E., Huck, M., Van Belle, S., & Di Fiore, A. (2020). The evolution of pair-living, sexual monogamy, and cooperative infant care: Insights from research on wild owl monkeys, titis, sakis, and tamarins. *American Journal of Physical Anthropology*, *171*, 118–173. https://doi.org/10.1002/ajpa.24017

Fernández-Duque, E., de la Iglesia, H., & Erkert, H. G. (2010). Moonstruck primates: Owl monkeys (*Aotus*) need moonlight for nocturnal activity in their natural environment. *PLoS One*, *5*(9), e12572. https://doi.org/10.1371/journal.pone.0012572

Fernandez-Duque, E., & de la Iglesia, H. O. (2023). Temporal niche plasticity of owl monkeys. *Owl Monkeys: Biology, adaptive radiation, and behavioral ecology of the only nocturnal primate in the Americas* (pp. 375–390). Springer International Publishing. https://doi.org/10.1007/978-3-031-13555-2_13

Fernandez-Duque, E., Juárez, C. P., & Defler, T. R. (2023). Morphology, systematics, and taxonomy of owl monkeys. *Owl monkeys: Biology, adaptive radiation, and behavioral ecology of the only nocturnal primate in the Americas* (pp. 3–23). Springer International Publishing. https://doi.org/10.1007/978-3-031-13555-2_1

Fernandez-Duque, E., Rotundo, M., & Ramirez-Llorens, P. (2002). Environmental determinants of birth seasonality in night monkeys (*Aotus azarai*) of the argentinean chaco. *International Journal of Primatology*, *23*(3), 639–656. https://doi.org/10.1023/A:1014929902923

Fernandez-Duque, E., Rotundo, M., Seltzer, J., Di Fiore, A., & Link, A. (2023). Past, present, and future use of technology for field studies of owl monkeys. *Owl monkeys: Biology, adaptive radiation, and behavioral ecology of the only nocturnal primate in the Americas* (pp. 325–352). Springer International Publishing. https://doi.org/10.1007/978-3-031-13555-2_11

Fernandez-Duque, E., Rotundo, M., & Sloan, C. (2001). Density and population structure of owl monkeys (*Aotus azarai*) in the argentinean chaco. *American Journal of Primatology*, *53*(3), 99–108. https://doi.org/10.1002/1098-2345(200103)53:3<99::AID-AJP1>3.0.CO;2-N

Gamba, M., Torti, V., Estienne, V., Randrianarison, R. M., Valente, D., Rovara, P., Bonadonna, G., Friard, O., & Giacoma, C. (2016). The indris have got rhythm! timing and pitch variation of a primate song examined between sexes and age classes. *Frontiers in Neuroscience*, *10*(249), 249. https://doi.org/10.3389/fnins.2016.00249

Garamszegi, L. Z. (2016). A simple statistical guide for the analysis of behaviour when data are constrained due to practical or ethical reasons. *Animal Behaviour*, *120*, 223–234. https://doi.org/10.1016/j.anbehav.2015.11.009

Garber, P. A., Pruetz, J. D., & Isaacson, J. (1993). Patterns of range use, range defense, and intergroup spacing in moustached tamarin monkeys (*Saguinus mystax*). *Primates*, *34*(1), 11–25. https://doi.org/10.1007/BF02381276

Garcia de la Chica, A., Spence-Aizenberg, A., Wolovich, C. K., Evans, S., & Fernandez-Duque, E. (2023). The social life of owl monkeys. In E. Fernandez-Duque (Ed.), *Owl monkeys: Biology, adaptive radiation, and behavioral ecology of the only nocturnal primate in the Americas* (pp. 391–422). Springer International Publishing. https://doi.org/10.1007/978-3-031-13555-2_14

Garcia de la Chica, A., Wood, D. B., Rotundo, M., & Fernandez-Duque, E. (2021). Responses of a pairliving, sexually monogamous primate to the simulated presence of solitary individuals: A field playback experiment. *Ethology*, *127*(11), 1002–1018. https://doi.org/10.1111/eth.13222

Harris, T. (2007). Testing mate, resource and infant defence functions of intergroup aggression in non-human primates: Issues and methodology. *Behaviour*, *144*(12), 1521–1535. https://doi.org/10.1163/156853907782512128

van der Heide, G., Fernandez-Duque, E., Iriart, D., & Juárez, C. P. (2012). Do forest composition and fruit availability predict demographic differences among groups of territorial owl monkeys (*Aotus azarai*)? *International Journal of Primatology*, *33*(1), 184–207. https://doi.org/10.1007/s10764-011-9560-5

Hilgartner, R., Fichtel, C., Kappeler, P. M., & Zinner, D. (2012). Determinants of pair-living in red-tailed sportive lemurs (*Lepilemur ruficaudatus*): Pair-living in red-tailed sportive lemurs. *Ethology*, *118*, 466–479. https://doi.org/10.1111/j.1439-0310.2012.02033.x

Hubbard, R., Haig, B. D., & Parsa, R. A. (2019). The limited role of formal statistical inference in scientific inference. *The American Statistician*, *73*(S1), 91–98. https://doi.org/10.1080/00031305.2018.1464947

Huck, M., & Fernandez-Duque, E. (2013). When dads help: Male behavioral care during primate infant development. *Building babies: Primate development in proximate and ultimate perspective* (pp. 361–385). Springer. https://doi.org/10.1007/978-1-4614-4060-4

Huck, M., & Fernandez-Duque, E. (2017). The floater's dilemma: Use of space by wild solitary azara's owl monkeys, *Aotus azarae*, in relation to group ranges. *Animal Behaviour*, *127*, 33–41. https://doi.org/10.1016/j.anbehav.2017.02.025

Huck, M., & Fernandez-Duque, E. (2023). The great unknown: The floating stage as a neglected aspect of social systems. *Owl monkeys: Biology, adaptive radiation, and behavioral ecology of the only nocturnal primate in the Americas* (pp. 461–496). Springer International Publishing. https://doi.org/10.1007/978-3-031-13555-2_16

Huck, M., Di Fiore, A., & Fernandez-Duque, E. (2020). Of apples and oranges? The evolution of “monogamy” in non-human primates. *Frontiers in Ecology and Evolution*, *7*, 472. https://doi.org/10.3389/fevo.2019.00472

Huck, M., Rotundo, M., & Fernandez-Duque, E. (2011). Growth and development in wild owl monkeys (*Aotus azarai*) of Argentina. *International Journal of Primatology*, *32*(5), 1133–1152. https://doi.org/10.1007/s10764-011-9530-y

Kappeler, P. M., & Pozzi, L. (2019). Evolutionary transitions toward pair living in nonhuman primates as stepping stones toward more complex societies. *Science Advances*, *5*(12), eaay1276. https://doi.org/10.1126/sciadv.aay1276

Kinnaird, M. F. (1992). Variable resource defense by the Tana River crested mangabey. *Behavioral Ecology and Sociobiology*, *31*(2), 115–122. https://doi.org/10.1007/BF00166344

Koch, F., Signer, J., Kappeler, P. M., & Fichtel, C. (2016). Intergroup encounters in verreaux's sifakas (*Propithecus verreauxi*): Who fights and why? *Behavioral Ecology and Sociobiology*, *70*, 797–808. https://doi.org/10.1007/s00265-016-2105-3

Korstjens, A. H., Nijssen, E. C., & Noë, R. (2005). Intergroup relationships in Western Black-and-White colobus, *Colobus polykomos polykomos*. *International Journal of Primatology*, *26*(6), 1267–1289. https://doi.org/10.1007/s10764-005-8853-y

Link, A., Muñoz-Delgado, J., & Montilla, S. O. (2023). Nocturnality and activity budgets of owl monkeys in tropical ecosystems. *Owl monkeys: Biology, adaptive radiation, and behavioral ecology of the only nocturnal primate in the Americas* (pp. 353–373). Springer International Publishing. https://doi.org/10.1007/978-3-031-13555-2_12

Majolo, B., DeBortoli Vizioli, A., Martínez-íñigo, L., & Lehmann, J. (2020). Effect of group size and individual characteristics on intergroup encounters in primates. *International Journal of Primatology*, *41*(2), 325–341. https://doi.org/10.1007/s10764-019-00119-5

Majolo, B., Ventura, R., & Koyama, N. (2005). Postconflict behavior among Male Japanese macaques. *International Journal of Primatology*, *26*(2), 321–336. https://doi.org/10.1007/s10764-005-2927-8

Martinez Inigo, L. (2018). *Intergroup interactions in crested macaques (Macaca nigra): Factors affecting intergroup encounter outcome and intensity* (Doctoral dissertation, University of Lincoln).

Mazerolle, M. J. (2020). Model selection and multimodel inference using the AICcmodavg package. *R Vignette*.

Mehlman, P. T., & Parkhill, R. S. (1988). Intergroup interactions in wild barbary macaques (*Macaca sylvanus*), ghomaran Rif mountains, Morocco. *American Journal of Primatology*, *15*(1), 31–44. https://doi.org/10.1002/ajp.1350150105

Moher, D., Liberati, A., Tetzlaff, J., & Altman, D. G. (2009). Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. *PLoS Medicine*, *6*(7), e1000097. https://doi.org/10.1371/journal.pmed.1000097

Norscia, I., & Borgognini-Tarli, S. M. (2008). Ranging behavior and possible correlates of pair-living in southeastern avahis (Madagascar). *International Journal of Primatology*, *29*(1), 153–171. https://doi.org/10.1007/s10764-007-9219-4

Ostfeld, R. S. (1990). The ecology of territoriality in small mammals. *Trends in Ecology & Evolution*, *5*(12), 411–415. https://doi.org/10.1016/0169-5347(90)90026-A

Overdorff, D. J., & Tecot, S. R. (2006). Social pair-bonding and resource defense in wild red-bellied lemurs. *Eulemur rubriventerLemurs: Ecology and Adaptation* (pp. 235–254). https://doi.org/10.1007/978-0-387-34586-4

Paré, G., Trudel, M., Jaana, M., & Kitsiou, S. (2015). Synthesizing information systems knowledge: A typology of literature reviews. *Information & Management*, *52*, 183–199. https://doi.org/10.1016/j.im.2014.08.008

Platt, J. R. (1968). Strong inference. *Science*, *161*(3841), 347–353. https://doi.org/10.1126/science.146.3642.347

Price, E. C., & Piedade, M. (2001). Ranging behavior and intraspecific relationships of masked titi monkeys (*Callicebus personatus personatus*). *American Journal of Primatology*, *53*(April 1999), 87–92. https://doi.org/10.1002/1098-2345(200102)53:2<87::AID-AJP4>3.0.CO;2-P

R Core Team, V. 4. 0. (2021). R: A Language and Environment for Statistical Computing. 5.

Reichard, U., & Sommer, V. (1997). Group encounters in wild gibbons (*Hylobates Lar*): Agonism, affiliation, and the concept of infanticide. *Behaviour*, *134*, 1135–1174. https://doi.org/10.1163/156853997X00106

Rosenbaum, S., Vecellio, V., & Stoinski, T. (2016). Observations of severe and lethal coalitionary attacks in wild mountain gorillas. *Scientific Reports*, *6*(1), 37018. https://doi.org/10.1038/srep37018

van Schaik, C. P. (1996). Social evolution in primates: The role of ecological factors and Male. *Behaviour. Proceedings of the British Academy*, *88*, 9–31.

Spence-Aizenberg, A., Williams, L. E., & Fernandez-Duque, E. (2018). Are olfactory traits in a pair-bonded primate under sexual selection? An evaluation of sexual dimorphism in *Aotus nancymaae*. *American Journal of Physical Anthropology*, *166*(4), 884–894. https://doi.org/10.1002/ajpa.23487

Steenbeek, R. (1999). Tenure related changes in wild thomas's langurs I: Between-Group interactions. *Behaviour*, *136*(5), 595–625. https://doi.org/10.1163/156853999501487

Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using akaike's information criterion. *Behavioral Ecology and Sociobiology*, *65*, 13–21. https://doi.org/10.1007/s00265-010-1037-6

Tecot, S. R., Singletary, B., & Eadie, E. (2016). Why “monogamy” isn't good enough. *American Journal of Primatology*, *78*(3), 340–354. https://doi.org/10.1002/ajp.22412

Thompson, F. J., Marshall, H. H., Vitikainen, E. I. K., & Cant, M. A. (2017). Causes and consequences of intergroup conflict in cooperative banded mongooses. *Animal Behaviour*, *126*, 31–40. https://doi.org/10.1016/j.anbehav.2017.01.017

Trivers, R. L. (1972). Parental investment and sexual selection. *Sexual selection and the descent of man: The darwinian pivot* (pp. 136–179). https://doi.org/10.4324/9781315129266-7

Wartmann, F. M., Juárez, C. P., & Fernandez-Duque, E. (2014). Size, site fidelity, and overlap of home ranges and core areas in the socially monogamous owl monkey (*Aotus azarae*) of Northern Argentina. *International Journal of Primatology*, *35*, 919–939. https://doi.org/10.1007/s10764-014-9771-7

Watts, D. P., Muller, M., Amsler, S. J., Mbabazi, G., & Mitani, J. C. (2006). Lethal intergroup aggression by chimpanzees in kibale national park, Uganda. *American Journal of Primatology*, *68*(2), 161–180. https://doi.org/10.1002/ajp

Whitten, P. L., Thompson, C. L., & Norconk, M. A. (2012). Why fight? selective forces favoring between-group aggression in a variably pair-living primate, the White-faced saki (*Pithecia pithecia*). *Behaviour*, *149*, 795–820. https://doi.org/10.2307/41720587

Williamson, E. A., & Feistner, A. T. C. (2003). Habituating primates: Processes, techniques, variables and ethics. *Field and Laboratory Methods in Primatology: A Practical Guide*. (2nd ed., pp. 33–50). https://doi.org/10.1017/CBO9780511921643.004

Wolf, K., & Schulman, S. R. (1984). Male response to “stranger” females as a function of female reproductive value among chimpanzees. *The American Naturalist*, *123*, 163–174.

Xiao, Y., & Watson, M. (2019). Guidance on conducting a systematic literature review. *Journal of Planning Education and Research*, *39*(1), 93–112. https://doi.org/10.1177/0739456X17723971

Yi, Y., Fichtel, C., Ham, S., Jang, H., & Choe, J. C. (2020). Fighting for what it's worth: Participation and outcome of inter-group encounters in a pair-living primate, the javan gibbon (*Hylobates moloch*). *Behavioral Ecology and Sociobiology*, *74*(8), 96. https://doi.org/10.1007/s00265-020-02879-0

Yi, Y., Fichtel, C., Kim, E., & Choe, J. C. (2020). Impacts of intergroup interactions on intragroup behavioral changes in javan gibbons (*Hylobates moloch*). *International Journal of Primatology*, *41*(2), 363–381. https://doi.org/10.1007/s10764-019-00116-8

Ziegler, T., Tecot, S. R., Fernandez-Duque, E., Savage, A., & Snowdon, C. T. (2022). Nonhuman primate paternal care: Species and individual differences in behavior and mechanisms. *Patterns of parental behavior—from animal science to comparative ethology and neuroscience* (pp. 213–238). Springer.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Gussone, L., García de la Chica, A., & Fernandez-Duque, E. (2024). Intergroup encounters in pair-living primates: Comparative analysis and a case study of pair-living and monogamous owl monkeys (*Aotus azarae*) of Argentina. *American Journal of Primatology*, *86*, e23572. https://doi.org/10.1002/ajp.23572