Predator-prey relationships of coyote (*Canis latrans*), ocelot (*Leopardus pardalis),* and puma (*Puma concolor*) in Costa Rican ecosystems

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Abstract: Evaluating predatory-prey relationships is critical for understanding the dynamics of ecosystems and implementing effective conservation efforts. I investigated whether Neotropical mammalian predators select prey based on relative abundance alone, on a subset of known prey species regardless of abundance, or on a combination of both. Data collected from camera traps located in seven sites in Costa Rica were used to calculate coefficients of overlapping (Δ) to assess the similarity of activity patterns between predators and their prey. Likelihood ratio tests were used to compare linear models of the three prey selection methods in which the dependent variable was Δ. Additionally, important prey species were identified for each predator using Δ, as well as the regression relationship of prey relative abundance index (RAI) and prey mass to Δ. The results indicated that coyote selected prey in relation to RAI, while both puma and ocelot hunted specific prey species, although puma were more strongly influenced by RAI.

Introduction

With declining populations of ocelot and puma, and the ever-expanding range of coyote (Kays, 2018; Nielsen et al., 2015; Paviolo et al., 2015; Vaughan-Dickhaut & Rodríguez-Sáenz, 1986), understanding the nature of the relationship between these predators and their prey is critical for informing comprehensive and effective conservation and mitigation efforts (Sinclair & Arcese, 1995). Past research on the predatory-prey relationships of puma, ocelot and coyote have concluded that all three predators are generally opportunistic and tend to hunt prey at rates consistent with the prey's relative abundance (Abreu et al., 2008; Emmons, 1987; Nowell & Jackson, 1996; Silva-Pereira et al., 2011). There are deviations in literature from this general designation, however. For each predator, specific prey are hunted in rates that do not reflect their relative abundance. Additionally, there is evidence that individuals hunt specific target prey due to individual preference or local adaptation, which is masked by the generalization of the species' hunting patterns. For example, the activity of leopards (*Panthera pardus*) varied from nocturnal in the African savannah to diurnal in the West African rainforest due to prey preference (Harmsen et al., 2011; Jenny & Zuberbühler, 2005).

Coyotes (*Canis latrans)* are a highly opportunistic canid predator that has been able to adapt to habitats that have been disturbed by human activity. This has enabled an expansion of their range by 40% since 1950 to extend throughout North America, Canada and Central America,

with the threat of extension into South America (Hody & Kays, 2018; Lariviere, 2019). Although coyote primarily hunt relative to abundance, research suggests that they use a combination of prey selectivity (by mass and prey species) and switching behavior (by abundance) (Randa et al., 2009). Coyote have been documented in Costa Rica, including in the highlands of Cerro de la Muerte (an important site within this study). In comparison to lowland observations, where coyote consumed mammals and reptiles (mainly collared peccary (*Pecari tajacu)* and iguana), prey consisted primarily of mammals (specifically cottontail rabbits) and birds at the higher elevations (Vaughan-Dickhaut & Rodríguez-Sáenz, 1986). In other parts of their range, they consume rodents, white-tailed deer (*Odocoileus virginianus)*, cottontail rabbits, skunk, and vegetation (Trani & Chapman, 2007). The full implication of coyote expansion is not fully known, although it is likely to detrimentally affect both Neotropical felids and mesopredators in the new regions (Cove, 2012; Gompper, 2002).

Ocelots (*Leopardus pardalis)* are a felid predator specialized in small, primarily mammalian prey species (de Villa Meza et al., 2009; Sunquist & Sunquist, 2002). Most prey species are less than 1 kg (Emmons, 1987; Ludlow & Sunquist, 1987; Murry & Gardner, 1997; Sunquist & Sunquist, 2002), although ocelot will also hunt larger species at lower frequencies (Bianchi et al., 2010). They are believed to be more efficient hunters on the ground compared with in the trees (Emmons, 1987; Ludlow & Sunquist, 1987; Murry & Gardner, 1997), with occasional consumption of arboreal species like tamandua and iguana (Abreu et al., 2008). The

most common species consumed are opossums, rodents, and cottontail rabbits (Abreu et al., 2008; Bianchi et al., 2010; Chinchilla, 1997; de Villa Meza et al., 2009; Emmons, 1987; Konecny, 1989; Ludlow & Sunquist, 1987; Sunquist & Sunquist, 2002; Wang, 2002). Ocelot hunt small mammals in relation to the prey's relative abundance with little selection of specific prey (Chinchilla, 1997; de Villa Meza et al., 2009; Emmons, 1987; Murry & Gardner, 1997), but hunt larger prey in a pattern that is the reverse of mass (Emmons, 1987; Sunquist & Sunquist, 2002). Ocelot prey selection has been studied extensively in specific regions, although this does not cover many parts of its range from Texas to Northern Argentina and is limited in Costa Rica (Chinchilla, 1997; González-Maya & Cardenal-Porras, 2011)

Pumas (*Puma concolor)* are a felid predator with a range that extends through North America, Central America and South America. In temperate regions, prey species primarily consist of large mammals, like white-tailed deer, in contrast to the small and medium-sized prey (1 to 15 kg) species in tropic regions (Chinchilla, 1997; Currier, 1983; Emmons, 1987; Sunquist & Sunquist, 2002). This includes rodents, porcupines, paca, peccary, and red brocket deer (*Mazama temama*) (Aranda & Sánchez-Cordero, 1996; Foster, Harmsen, Valdes, Pomilla, & Doncaster, 2010; Núñez, Miller, & Lindzey, 2000; Scognamillo, Maxit, Sunquist, & Polisar, 2003). Previous research has found evidence that puma are not strictly opportunistic predators that hunt in rates proportional to the relative abundance of the prey. Consumption of agouti and paca occurs in rates similar to their respective relative abundance, but consumption of red brocket deer is independent of abundance (Harmsen et al., 2011). Additionally, some literature has found puma to hunt specific prey at consistent rates across sites, regardless of changes in prey relative abundance (Elbroch & Wittmer, 2013; Novack, Main, Sunquist, & Labisky, 2005). This shows a tendency for higher selectivity than would be predicted if puma was strictly opportunistic.

I investigated predator-prey relationships of puma, ocelot and coyote across seven lowland, midland and highland sites in Costa Rica to determine if prey was selected based on relative abundance alone, on a subset of known prey species regardless of abundance, or on a combination of both. Additionally, important prey species were identified for each predator using coefficients of overlapping (Δ) and the regression relationship of prey relative abundance index (RAI) and prey mass to Δ. The hypothesis was that all three

predators would preferentially hunt prey species with high relative abundance.

Methods

Study Area
In collaboration with national park guards, community volunteers, and local conservation groups, this study was conducted across seven sites in the lowland, midland and highland regions of Costa Rica, each including multiple surveys in national parks, biological corridors and private reserves. The seven sites (Fig. 1) included four highland parks and reserves (names within brackets represent shortened names used within this paper): Tapantí Macizo de la Muerte National Park [Tapanti], Savegre Lodge Private Reserve [Savegre], Chirripo National Park [Chirripo], and La Amistand International Park [PILA]. Additionally, there were
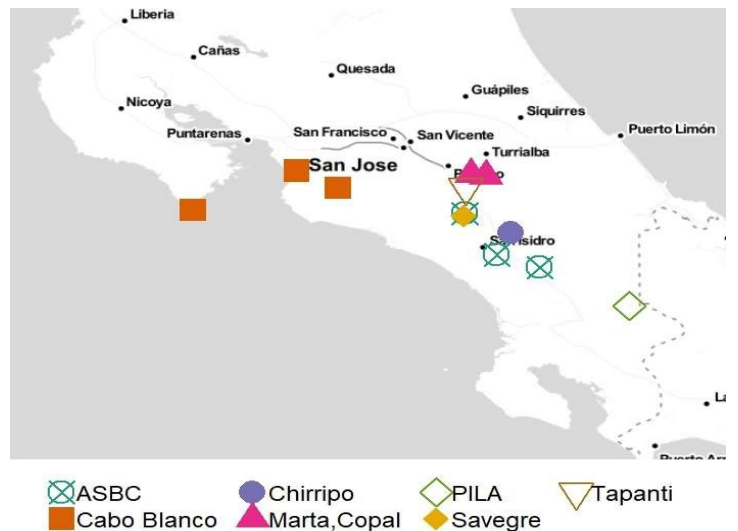

Figure 1: **Map of Sites.** *Each individual survey is mapped by coordinates. Its shape corresponds to site designation. See Appendix C for details on camera days, coordinates, elevation, environment, and dates.*

three lowland/midland sites: La Marta National Wildlife Refuge and El Copal Private Reserve [Marta, Copal], Alexander Skutch Biological Corridor, Bosque de Agua Biological Corridor, and Los Cusingos Bird Sanctuary [ASBC], and Cabo Blanco National Park, La Congreja National Park, and Carara National Park [Cabo Blanco]. Across sites, rainfall varied from 300 to 800 cm per year and temperature varied from 10-20°C in the highlands and 24-32°C in the lowlands ("CostaRica.com", 2019). All sites were characterized by two distinct seasons, with the dry season lasting from December to April and the wet season from May to November.

Camera Traps and Scent Stations
Camera trap studies have become increasingly widespread and can be used to measure activity patterns, abundance, and predator-prey temporal interactions (Carbone et al.,

1995; Di Bitetti et al., 2006; Harmsen et al., 2011; Herrera et al., 2018; Karanth, 1995; Maffei et al., 2005; Trolle & Kéry, 2005; Wallace et al., 2003). Cameras in each site were deployed for varying time periods from June 2010 to May 2018, restricted by when researchers and collaborators were able to maintain the cameras. Bushnell Trophy Cam™ units (the models changed over the years) were deployed either as single units or as paired camera stations to image both sides of the animal. The Bushnell Trophy Cam™ has a passive infrared sensor (PIR) and a fast trigger speed in response to heat and movement within a 75° detection angle and a 42° field of range (Bushnell Corporation, Lenexa, KS, USA). We avoided using cameras with incandescent white flash because it startles animals and contributes to avoidance behavior (Séquin et al., 2003). The cameras were equipped with a 2-8 GB SanDisk SD memory card (Western Digital Technologies, Milpitas, CA, USA) and Ultimate lithium AA batteries (Energizer Holdings, St. Louis, MO, USA), along with silica desiccant capsules (DRICAP capsule dehydrators; Ted Pella Inc., Redding, CA, USA) to minimize humidity inside the camera. Cameras were attached primarily to trees approximately 1 meter from the ground with Python 3/8" cable locks (Master Lock Company, Oak Creek, WI, USA) within steel security boxes (CAMLOCKbox, Green Bay, WI, USA). Each station was placed 1-2km apart along trails and access roads, pointed down the trail to maximize the time the individual animal was positioned within the camera's field of view. Garmin eTrex GPS units (Garmin Ltd., Olathe, KS, USA) were used to record the coordinates and elevation of each camera station.

The majority of camera stations had scent stations within the field of view to stimulate passing animals to slow down and investigate the novel scent. Scent stations are an efficient method widely used to increase photo quality for studies aimed at occupancy calculations, animal identification, and hair collection (Barea-Azcón et al., 2007; Conner et al., 1983; Randel & D. Peace, 2010; Thorn et al., 2009; Travaini et al., 1996; Weaver et al., 2005). Because less light is produced by infrared flash compared to the white flash, the scent stations were beneficial in maximizing the quality and minimizing blurriness of the photos. Each station consisted of either a free-standing PVC pipe, or a strap attached to a tree, with a piece of sponge scented with 4-5 sprays of Calvin Klein's Obsession cologne (Calvin Klein's 'Obsession for Men'; Calvin Klein Inc. New York, NY, USA) (Myers & Main, 2013) inside a clear plastic tube. The scent can only be detected at short range on the trail, thus scent stations do not attract animals that are not already on the trail. Studies have found that scent stations do not affect temporal activity, distance traveled, or total photographic capture (Braczkowski et al., 2016).

Database
Photographs from camera stations were tagged with a date and time, manually sorted into folders by species and site, then loaded into Camera Base 1.7 data management software (Tobler, 2015). Photographic records of a species were considered independent if photos were at least 30 minutes apart (Ridout & Linkie, 2009). Photographs of multiple individuals of the same species were classified as a single observation, as were photographs from paired cameras. Data was exported from Camera Base into an Excel .csv file for analysis. Tables of sample sizes, times of deployment, etc

Data Analysis
Activity Patterns and Δ
All analysis was done in the R programming language (R Core Team, 2017). To determine the overlap of activity budget between the predator and prey species at each site, the package Overlap was used following the two-step method developed by Ridout and Linkie (2009). First, the daily activity patterns were determined using either a kernel density with a standard bandwith of 1 and a bandwidth adjustment of 0.8 for large sample sizes (n>75), or with a non-negative trigonometric sum distribution for small sample sizes (20≤n≤75) (S. Ridout & Linkie, 2009). The minimum sample size was set at 20 independent observations to minimize overestimation of Δ (discussed below) (Lynam et al., 2013; Rowcliffe et al., 2014; Tan et al., 2018). This calculation used the standard assumptions that observations were regarded as random samples from a continuous distribution and that it was equally likely to capture an animal at any time during the period when they were active (Ridout & Linkie, 2009). Next, the coefficient of overlapping (Δ) was calculated, either using the $Δ_1$ measure for small sample sizes or $Δ_4$ for large sample sizes. The Δ values fall between 0 (no overlap) to 1 (complete overlap) and represent the shared area under two density curves. The average of Δ for each predator-prey pair was calculated by finding the mean Δ across all sites. For this study, Δ was used to assess the strength of predator-prey relationship and identify prey species important to the predator's diet. A Δ of 0.7 or higher was considered to represent a strong relationship *(Lynam et al., 2013;* Mugerwa et al., 2017*)*. This was based on the assumption that the activity of the predator reflected the preys' activity, with the greatest amount of circadian Δ occurring with the prey species most

important to their diet (Emmons, 1987; Fedriani et al., 1999; Harmsen et al., 2011; Herrera et al., 2018; Linkie & Ridout, 2011; Quigley, 1987; Rabinowitz & Nottingham, 1986; Ridout & Linkie, 2009). This was supported by characteristic hunting activity of these predators using auditory and visual cues to track prey, so hunting occurs when the prey species is foraging (Harmsen et al., 2011; Kitchener, 1991; Sunquist & Sunquist, 2002).

Relative Abundance Indices

Common prey species for each predator analyzed were narrowed down to known prey through a literature search of scat analysis studies (summarized in Table 1). These prey species do not include arboreal, rodent, reptile or bird species due to the nature of the camera trap study.

*Table 1: **Prey Species for Each Predator.** Known prey for each predator was determined through a literature search of scat analysis studies * represents species that are found commonly in scat samples of that predator.*

Coyote	Dice's Cottontail (*Sylvilagus dicei*), Armadillo (*Dasypus novemcinctus*), Central American Red Brocket Deer (*Mazama temama*), Collared Peccary (*Pecari tajacu*), White-tailed Deer (*Odocoileus virginianus*), Coati (*Nasua narica*)
Ocelot	Rodents (*Rodentia*), Central American Agouti* (*Dasyprocta punctata*), Tamandua (*Tamandua mexicana*), Armadillo* (*Dasypus novemcinctus*), Raccoon (*Procyon lotor*), Coati (*Nasua narica*), Collared Peccary (*Pecari tajacu*), Opossums (*Didelphidae*), Tayra (*Eira barbara*), Common Gray Four-eyed Opossum (*Philander opossum*), Dice's Cottontail (*Sylvilagus dicei*), Paca (*Cuniculus paca*), Central American Red Brocket Deer (*Mazama temama*)
Puma	Rodents (*Rodentia*), White-tailed Deer (*Odocoileus virginianus*), Armadillo (*Dasypus novemcinctus*), Dice's Cottontail (*Sylvilagus dicei*), Collared Peccary* (*Pecari tajacu*), Raccoon (*Procyon lotor*), Coati (*Nasua narica*), Paca* (*Cuniculus paca*), Coyote (*Canis latrans*), Striped Hog-nosed Skunk (*Conepatus semistriatus*), Central American Red Brocket Deer* (*Mazama temama*), Tamandua (*Tamandua mexicana*), Armadillo (*Dasypus novemcinctus*), Central American Agouti* (*Dasyprocta punctata*), Opossums (*Didelphidae*), Porcupine (*Coendou mexicanus*), Common Gray Four-eyed Opossum (*Philander opossum*)

Abreu et al., 2008; Aranda et al., 1995; Ávila-Nájera et al., 2018; Bianchi et al., 2010; Cruz-Espinoza et al., 2010; Foster et al., 2009; Gómez-Ortiz & Monroy-Vilchis, 2013; Grajales-Tam & González-Romero, 2014; Hernández-Saintmartín et al., 2015; Hidalgo-Mihart et al., 2009; Martinez et al., 2010; Medellín et al., 2002; Monroy-Vilchis et al., 2009; Moreno et al., 2006; Novack et al., 2005; Rueda et al., 2013; Scognamillo et al., 2003; Silva-Pereira et al., 2011; Wainwright, 2002.

The relative abundance indices (RAI) were calculated for each species at each of the seven sites using the equation:

$$RAI = \frac{sample\ size}{days\ camera\ was\ active} * 1000 \ .$$

These relative abundance indices may be biased by differential detection rates due to characteristic activity, size of home range, and interaction with camera stations (Sollmann et al., 2013). In statistical tests, the RAI was transformed with a logarithm base 10 to increase normality of the RAI variable. Linear regressions were used to assess the relationship between RAI and Δ for each predator. Any violation of assumptions was tested with homogeneity and normality plots, as well as Levene's and Fligner-Killeen tests of homogeneity and Shapiro-Wilke tests for normality (Appendix A).

Mass Advantage

A value termed *mass advantage* was calculated for each prey species by dividing the mass of the prey by the mass of the predator. Small values represented prey species that were small in comparison to the predator, while values greater than 1 represented species larger than the predator. This was used instead of the raw mass of the prey so that the size relationship to the predator was standardized. A linear regression was used to assess the relationship between mass advantage and Δ. Any violation of assumptions was tested as previously outlined (Appendix A).

Model Selection

The optimal model for the generalized predator-prey relationship for each predator was determined using likelihood ratio tests to compare linear regression models (using the lm function in R) following the recommended top-down strategy (Zuur, 2009). The explanatory variables being assessed were the numerical variable of RAI and the categorical variable of prey species. The starting point was a linear regression model containing both explanatory variables including the interaction between the two. Using a likelihood ratio test, the significance of the interaction term when dropped was determined. If the p-value was not significant, the interaction was dropped from the model, leaving the two variables without the interaction. Then likelihood ratio tests were used to determine the significance when each variable was dropped from the model. Again, if the p-value was not significant the variable was dropped from the model. The initial and final models were both tested for violation of assumptions as previously outlined (Appendix A).

Results

Coyote

For brocket deer, white-tailed deer and cottontail, the average coefficients of overlapping (Δ) with coyote were greater than 0.6. (Table 2). Armadillo, coati, and peccary had an average Δ below 0.6, and no prey species had an average
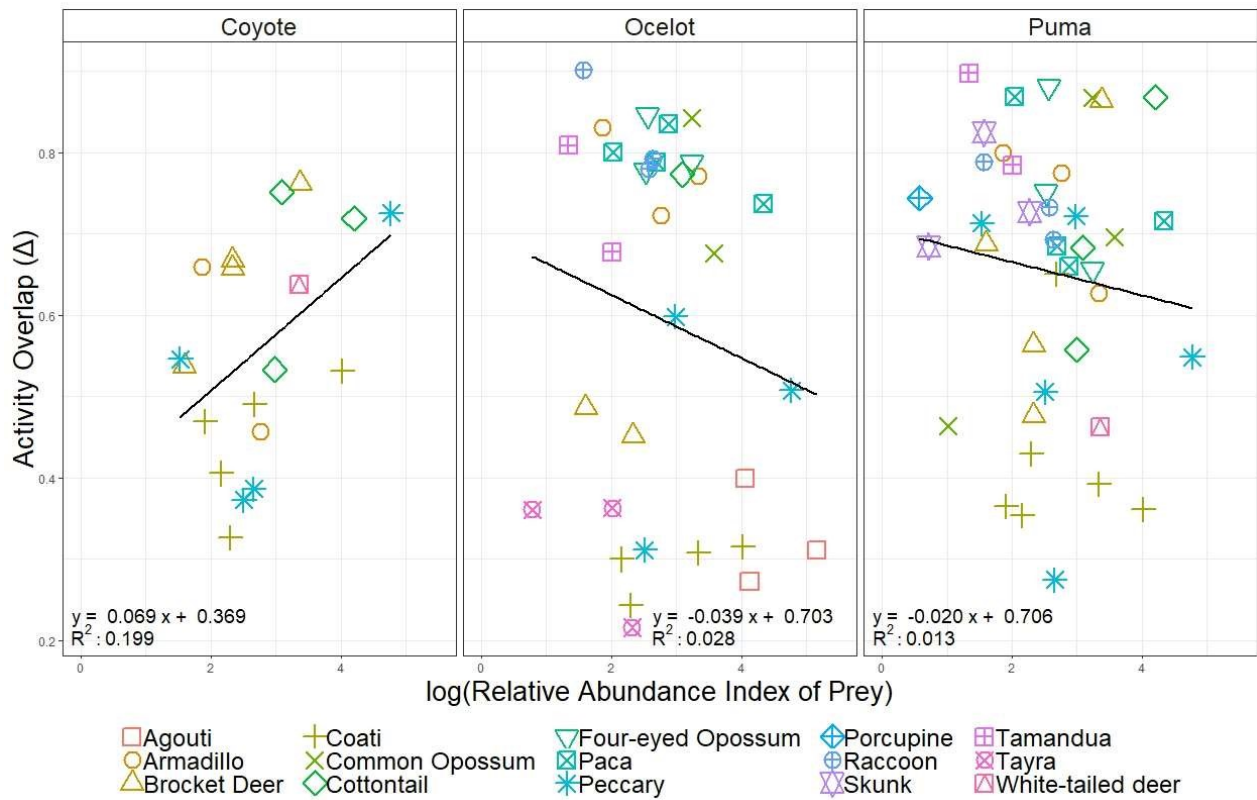
*Figure 2: **Relationship between RAI and Δ.** Plot of the relationship between RAI of prey with a log transformation and Coefficient of Overlapping (Δ) for each predator species.*
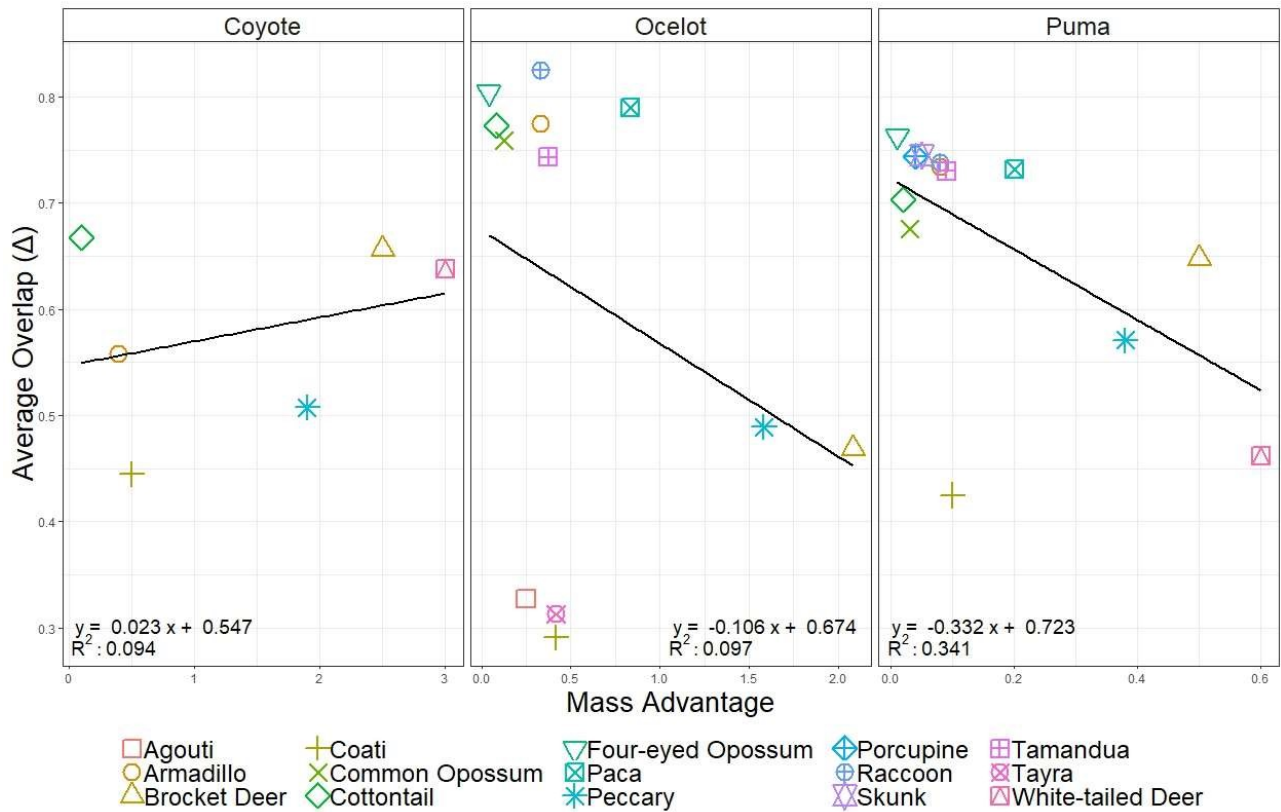

*Figure 3: **Relationship between mass advantage and average Δ.** Plot of the relationship between mass advantage of each specific prey (mass of prey/mass of predator) and average Coefficient of Overlapping (Δ) for each predator.*

Δ above 0.7 (Table 2). Overall, there was a positive relationship between prey RAI and Δ for coyote, with 20% of the variation in Δ explained by the regression (Fig. 2) [the linear model did not violate normality or independence, although there was slight violation of homogeneity with variation of spread in residuals and a Fligner-Killeen p-value of 0.047 (Fig. 2 in Appendix A)].

Table 2: **Average Δ Shows Strength of Predator-Prey Relationships.** The average coefficient of overlapping (Δ) of all sites and mass advantage (prey mass divided by mass of predator for each prey species in relation to the predator species.

Predator Species	Prey Species	Average Δ	Mass Advantage
Coyote	Cottontail	0.668	0.100
	Brocket Deer	0.656	2.500
	White-tailed Deer	0.638	3.000
	Armadillo	0.558	0.400
	Peccary	0.508	1.900
	Coati	0.445	0.500
Ocelot	Raccoon	0.825	0.333
	Four-eyed Opossum	0.804	0.042
	Paca	0.790	0.833
	Armadillo	0.775	0.333
	Cottontail	0.773	0.083
	Common Opossum	0.759	0.125
	Tamandua	0.743	0.375
	Peccary	0.489	1.583
	Brocket Deer	0.469	2.083
	Agouti	0.327	0.250
	Tayra	0.313	0.417
	Coati	0.291	0.417
Puma	Tamandua	0.841	0.090
	Four-eyed Opossum	0.763	0.010
	Skunk	0.745	0.050
	Porcupine	0.744	0.040
	Raccoon	0.738	0.080
	Armadillo	0.734	0.080
	Paca	0.732	0.200
	Cottontail	0.703	0.020
	Common Opossum	0.676	0.030
	Brocket Deer	0.648	0.500
	Peccary	0.571	0.380
	Wite-tailed Deer	0.462	0.600
	Coati	0.425	0.100

In general, the species with the highest RAI at each site had the highest Δ with coyote (Fig. 4). At Cabo Blanco, peccary had the highest RAI at 118.125 and highest Δ at 0.725. The same followed for cottontail at Chirripo [RAI=66.843, Δ =0.718] and Savegre [21.963, 0.751], and brocket deer at Tapanti [29.311, 0.762] (Fig. 4, individual RAI and Δ values found in Appendix B). Beyond the highest RAI, there was not necessarily a pattern of increased Δ corresponding to higher RAI. At Cabo Blanco, for example, brocket deer had the lowest RAI [10.312] but second highest Δ [0.668], while coati had the second highest RAI [55.625] but second lowest Δ
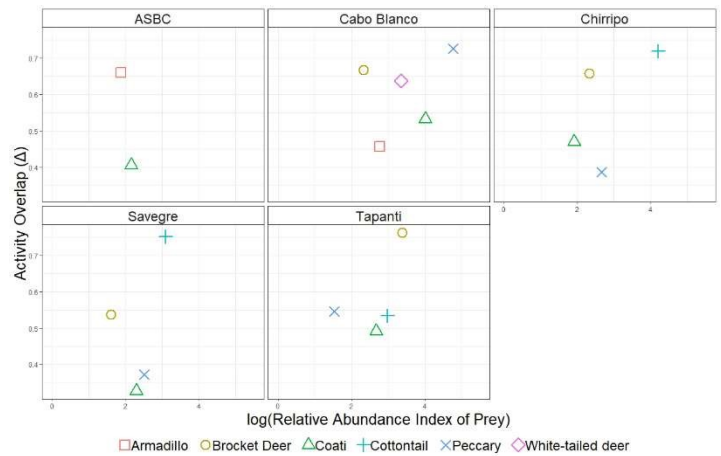

Figure 4: **Predator-Prey Relationship at Each Site for Coyote.** The relationship of RAI of prey with a log transformation and Coefficient of Overlapping (Δ) at each site.

[0.532] (Fig. 4, individual RAI and Δ values found in Appendix B). Similar patterns were seen at the other sites.

There was little correlation between mass advantage and the average Δ. Across all sites, the linear model between the average Δ and mass advantage accounted for 0.5% of the variation in average Δ and in general the average Δ did not vary in a pattern determined by mass of the prey (Fig. 3). Cottontail and brocket deer had similar average Δ [0.668 and 0.656 respectively], but significantly different mass advantages [0.1 and 2.5 respectively] (Fig. 3).

From the model selection, the optimal model was the prey RAI [as mentioned previously, the model was valid within reason (Appendix A)]. The removal of interactions between RAI and Species was not significant with a p-value of 0.126, so was omitted from the linear model (Table 3). The variable prey species was not significant with a p-value of 0.0765 when removed so was omitted from the model. The variable prey RAI was significant with a p-value of 0.0447 when removed, although this was not much below the alpha of 0.05 (Table 3).

Table 3: **Model Selection of Predator-Prey Relationships.** P-values were calculated using likelihood ratio tests to determine the significance of removing a variable from the full model. A significant P-value (bold) means that the variable should not be omitted from the model. Prey RAI * Species signifies the interaction term in the full model.

	Prey RAI * Species	Prey Species	Prey RAI
Coyote	0.126	0.0765	**0.0447**
Ocelot	**<0.001**	**<0.001**	0.411
Puma	**0.050**	**0.004**	0.207

Ocelot

The average Δ between ocelot and raccoon, four-eyed opossum, paca, armadillo and cottontail were above 0.7 and remained above 0.7 regardless of the RAI at each site (Table 2). Common opossum and tamandua both had an average Δ above 0.7 (0.759 and 0.743 respectively) and remained above 0.67 across all sites regardless of RAI (Table 2). The average Δ of other known species were below 0.5 (Table 2). Overall, there was little relationship between prey RAI and Δ, with 2.8% of the variation in Δ explained by RAI (Fig. 2) [the linear model was not appropriate with violations of normality (Fig. 5 in Appendix A)]. Specific species had a relatively constant Δ with ocelot despite differences in RAI as seen in Fig. 3. For example, coati had a range in RAI of 8.638 to 55.625 and a range of Δ from 0.243 to 0.315 (Fig. 2, values of RAI and Δ found in Appendix B).
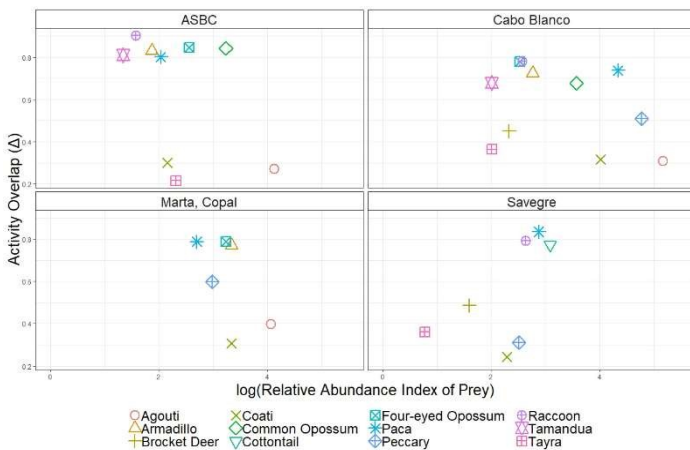

Figure 5: **Predator-Prey Relationship at Each Site for Ocelot.** *The relationship of RAI of prey with a log transformation and Coefficient of Overlapping (Δ) at each site.*

At each site there was little relationship between prey RAI and Δ (Fig. 5). At ASBC, coati, tayra, and agouti had Δ at or below 0.3, although their RAI spread from 8.638 (coati) to 62.126 (agouti) (Fig. 5, individual values in Appendix B). On the other hand, tamandua, raccoon, armadillo, paca, four-eyed opossum, and common opossum had Δ at or above 0.8, although their RAI spread from 3.821 (tamandua) to 25.415 (common opossum). At Cabo Blanco and Marta/Copal a similar pattern was seen, with the largest RAI corresponding to the one of the lowest Δ and the inverse being true for the smallest RAI (Fig. 5). At Savegre, there was some correlation between RAI and Δ, with the three species raccoon, paca and cottontail that had the highest Δ, also had high RAI (Fig. 5). This may have had little to do with RAI since these species consistently have high Δ at other sites.

There was little linear correlation between mass advantage and average Δ, with 9.7% of the variation in Δ explained by

mass advantage (Fig. 3) [the model violated homogeneity and normality, (Fig. 7 in Appendix A)]. Instead, there were clustering of species with small mass advantage and high Δ, species with large mass advantage and low Δ, and species with small mass advantages and low Δ (Fig. 3). The species with average Δ greater than 0.7 had mass advantages smaller than 0.375 (tamandua), except for paca which had a mass advantage of 0.833 when fully grown (Table 2). Not all species with low mass advantage have high Δ, as agouti, coati and tayra had low Δ despite having low mass advantages.

From the model selection, the optimal model was the full model with the interaction between prey RAI and prey species [normality violated (Fig. 4 in Appendix A]. The removal of interaction between RAI and Species was significant with a p-value of <0.001 (Table 3). The variable prey species was significant when removed, while the prey RAI was not significant (Table 3).

Puma

The average Δ was over 0.7 for tamandua, four-eyed opossum, skunk, porcupine, raccoon, armadillo, paca, and cottontail (Table 2). Of these, all had Δ above 0.6 at each site regardless of RAI, except cottontail which had an overlap of 0.558 at Tapanti (Appendix B). Overall, there was little linear correlation between Δ and prey RAI with 1.3% of variation in Δ accounted for by RAI (Fig. 2) [the linear model violated normality, although did not violate homogeneity or independence (Fig. 9 in Appendix A)].
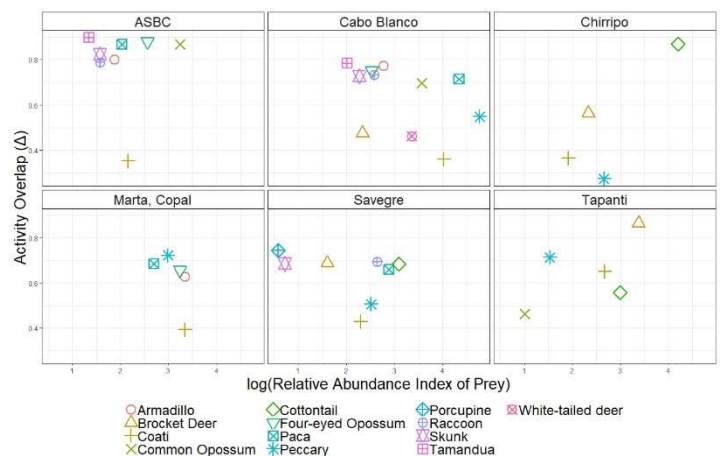

Figure 6: **Predator-Prey Relationship at Each Site for Puma.** *The relationship of RAI of prey with a log transformation and Coefficient of Overlapping (Δ) at each site.*

At ASBC, there was little relationship between RAI and Δ (Fig. 6). All species, except for coati, had high overlap near 0.8. At Cabo Blanco, there was little linear relationship between Δ and RAI with Δ spread across regardless of RAI (Fig. 6). At Chirripo, cottontail had the largest RAI and the

highest Δ, significantly higher than other prey species relationship between RAI and Δ with most about 0.6-0.7 present. Like at ASBC, Marta and Copal had little except for coati at 0.392 (Fig. 6, individual values found in Appendix B). Savegre as well had little linear relationship, with most Δ clustered regardless of RAI. At Tapanti the lowest and highest RAI corresponded to the lowest and highest Δ respectively. Brocket deer had a Δ of 0.864 with a RAI of 29.311, while common opossum had a Δ of 0.464 and a RAI of 2.755 (Fig. 6, values found in Appendix B). Interestingly, this higher Δ for brocket deer at Tapanti was connected to a significant deviation in puma activity pattern compared to other sites (Fig. 7). Puma had an abnormal peak of activity
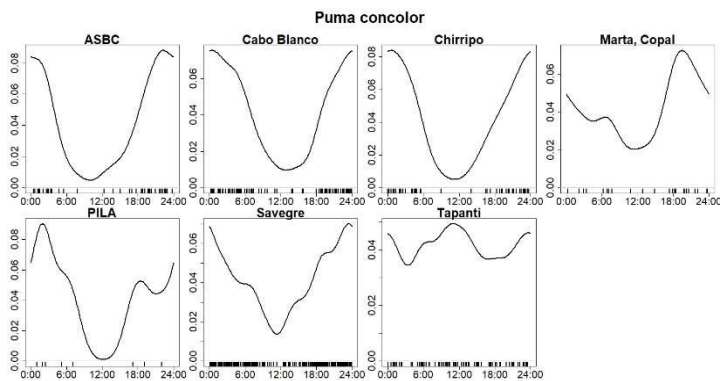

*Figure 7: **Activity Budget of Puma at the seven sites**. The predator is primarily cathemeral, although shows deviating activity pattern at Tapanti with an increased diurnal activity.*

during the daylight hours, mirroring the diurnal activity of brocket deer.

There was a linear relationship between average Δ and mass advantage, with 34% of variation in average Δ accounted for by mass advantage (Fig. 3) [linear model violated normality and homogeneity (Fig. 11 in Appendix A)]. All species with average Δ above 0.7 had mass advantages under 0.1, except for Paca which had a mass advantage of 0.2. Common opossum had a mass advantage of 0.3 and an average Δ close to 0.7 at 0.676. An exception to the relationship was coati with a mass advantage of 0.1 but an average Δ of 0.425 and brocket deer with a mass advantage of 0.3 and an average Δ of 0.648 (Table 2).

From the model selection using a likelihood ratio test, the optimal model was the full interaction model [normality violated (Fig. 8 in Appendix A)]. The removal of interaction between RAI and Species was close to significant at an alpha of 0.05, so was not omitted from the model (Table 3). The variable Prey Species was significant when removed with a p-value of 0.00447, while RAI was not significant when removed with a p-value of 0.207 (Table 3).

Discussion:

In general, coyote are generalists that follow a prey selection strategy primarily based on the RAI of the prey species. The highest Δ was seen with the prey species that had the highest RAI at each site, suggesting that prey switching occurred. The prey RAI and Δ correlation did not extend to other prey species at each site with lower RAI, so coyote was primarily focusing on the prey with the highest RAI only. The species most important to the diet of coyote were brocket deer and cottontail based on average Δ. Brocket deer had the highest RAI and Δ at Tapanti, and cottontail had the highest RAI and Δ at Savegre and Chirripo, all highland locations. Peccary was another species that was important at one site, specifically the lowland Cabo Blanco site, although had a low Δ at other sites. This was consistent with past research (Randa et al., 2009; Vaughan-Dickhaut & Rodríguez-Sáenz, 1986). Additionally, there was no preference for species with specific mass advantages for coyote.

In general, ocelot preyed on specific species across all sites. Although the model selection resulted in the interaction of species and RAI as the optimal model, the majority of sites analyzed showed little change or a decrease in Δ as RAI increased. The influence of RAI on prey selection that the test recognized was likely this negative linear relationship. Additionally, across sites the same species consistently had high overlaps regardless of their RAI. Interestingly, this seemingly contradicts the majority of research showing that ocelot hunt small prey species in relation to RAI (Chinchilla, 1997; de Villa Meza et al., 2009; Emmons, 1987; Murry & Gardner, 1997). This deviation is likely due to the consistently high RAI of the two opossum species, creating the aberration of no relationship between RAI and Δ. For larger prey, past research determined that there is no pattern following relative abundance, although in this study there was no clear relationship between mass and Δ as would be suggested (Emmons, 1987; Sunquist & Sunquist, 2002). The species most important to the ocelot diet were tamandua, armadillo, common opossum, four-eyed opossum, paca, raccoon, and cottontail as they had high Δ at each site regardless of RAI, consistent with prior literature (Abreu et al., 2008; Bianchi et al., 2010; Chinchilla, 1997; de Villa Meza et al., 2009; Emmons, 1987; Konecny, 1989; Ludlow & Sunquist, 1987; Sunquist & Sunquist, 2002; Wang, 2002). As many small prey species, like rodents, birds and reptiles, were not included in this study, these findings do not contradict the classification of ocelot as a specialist in

small prey (de Villa Meza et al., 2009; Sunquist & Sunquist, 2002). It does however support the conclusion that large prey species can also be important parts of ocelot's diet (Bianchi et al., 2010).

Puma primarily hunted specific prey species, although relative abundance had influence for certain species at specific sites. This is consistent with findings that puma is opportunistic, although does practice preferential prey selection (Elbroch & Wittmer, 2013; Novack et al., 2005). Based on average Δ, puma preferred tamandua, four-eyed opossum, skunk, porcupine, raccoon, armadillo, paca and cottontail. Puma demonstrated prey switching based on RAI of the prey species, specifically seen at Tapanti and Chirripo. At these sites, puma hunted brocket deer and cottontail respectively at higher frequencies (represented by high overlap), corresponding to high relative abundance of the prey species and absence of other preferred prey species. For example, at Tapanti this individual preference for brocket deer may have been due to common opossum having a significantly lower RAI compared to other sites, resulting in puma being forced to hunt other species. Or it may have been due to brocket deer having a high RAI compared to other sites and puma preferentially hunting them. Likely it was a combination of both, and resulted in a distinct change in puma activity pattern. This trend has been seen at other locations, where puma activity was observed later into the morning corresponding to the activity of the abundant brocket deer (Aranda & Sánchez-Cordero, 1996; Harmsen et al., 2011). Common opossum is likely another species preferentially hunted by puma since, when Tapanti is removed as an outlier, the average Δ was 0.782. All these preferred species had masses below 5 kg (mass advantage of 0.1).

A limitation to this study was that the prey species analyzed did not include arboreal, rodent, reptile, or bird species, so respective predator-prey relationships were not explored. They are likely to follow similar trends since the predation strategy is a nature of the predator, although which specific species would be important to the predator's diet could not be predicted from these conclusions. Additionally, due to the calculation of Δ per site, which required a minimum sample size of 20 individual observations, the number of Δ observations per predator was smaller than desired. Also, Δ

for each species may not be entirely independent of the Δ of another species. If the activity budgets of two prey species were similar, then closer alignment of predator activity to one specific prey species would also increase the Δ the other prey regardless if the predator was hunting that species. These implications of using Δ may have limited the strength of the regression statistics and linear model selections.

To address these limitations, the deployment of more cameras at both existing and additional sites would increase the number of observations analyzed and the strength of the statistical tests. This would also allow the use of mixed-effects modelling, which includes random effects in the model to account for non-independence between sites, limiting false positives and negatives (Harrison et al., 2018). To complement this study, a dietary analysis of scat at each site would confirm the strength of Δ in predicting prey preference.

Understanding these aspects of predator-prey relationships informs conservation and impact management for the predator species discussed. The results imply that the key to successful conservation efforts for puma and ocelot populations is the preservation of the main prey species, specifically those identified in this paper. Insight into the variation between sites of which prey species supports the predator population enables conservation efforts to be tailored to each location.

In mitigating the impacts of coyote's range expansion, it is important to understand that coyote preferentially hunt the most abundant prey species, indicating that coyote is less specialized than puma and ocelot. This allows the species to more readily adapt to new habitats, as well as to environmental changes within their existing range. Coyote are known to outcompete other predatory species (Fuller, 2002; Litvaitis, 1989; Springer et al., 2012), which in the Talamanca Cordillera may predict potential decline of puma and ocelot populations in the future. This is especially probable as many of the prey species hunted by coyote at each site overlapped with the preferred prey of puma and ocelot. It is critically important to monitor the expansion of coyote into these new locations. More research is needed to illuminate the relationship between coyote and the native predators, as well as the long-term implications of and potential management strategies to control and prevent coyote's range expansion.

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Appendix A: Linear Model Validation

Data Cleaning:

Data: Relative abundance indeces and coefficients of overlapping calculated on the data collected as of May 2018 using a minimum sample size of 20 to calculate the coefficent. Mass advantage is the mass of the prey divided by the mass of the predator. A smaller value represents a small prey species that the predator will have a greater advantage over.

Looking at the linear models with mass advantage or prey relative abundance index compared to coefficient of overlapping for each predator, the model was assessed. Residual vs fitted value plots assessed homogeneity, qqnorm plots of residuals assessed normality, and Residuals versus each variable assessed independence and homogeneity. Levene's Test (more resistant to nonnormality than Bartlett's Test) and Fligner-Killeen tests (most resistant to nonnormality of the three tests) were used to assess homogeneity, while Shapiro-Wilke tests were used to assess normality.

Model Validation for Linear Model Selection

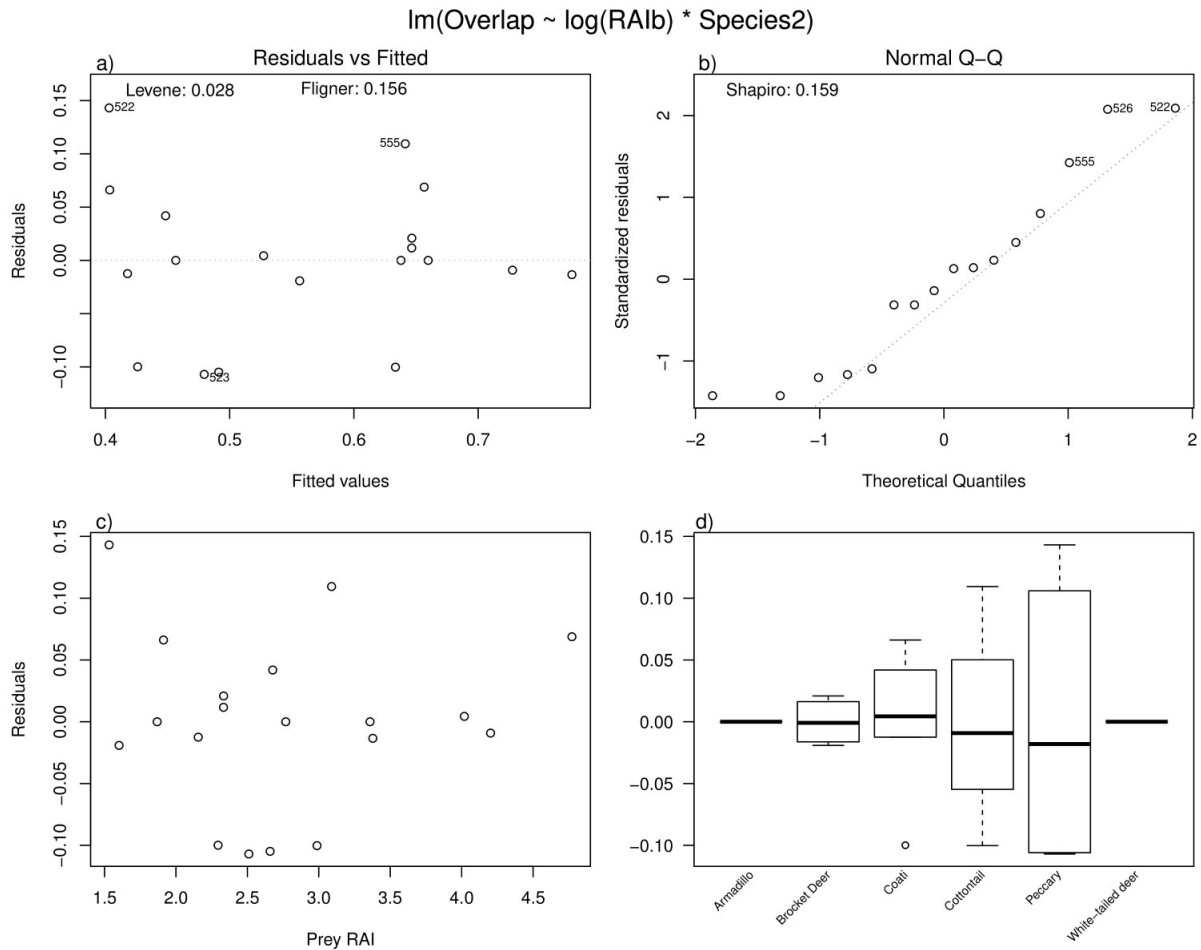**Coyote: Full Model (lm(Overlap~log(Prey RAI)*Prey Species))**

Figure 1: Model validation graphs for full model: Prey RAI * Prey Species. a) Fitted values versus residuals to assess homogeneity. There was variation in spread of residuals for each fitted value. The Levene p-value is signficant, but the Fligner-Killeen p-value (more resistant to) is not significant. b) QQnorm plot of residuals. Normality not violated with residuals close to normal line without any pattern. Shapiro-Wilke p-value is not signficant either. c) Residuals vs log(Prey RAIb). Independence not violated, although homogeneity is with log(RAI) of 3 having a different spread. d) Residuals versus prey specie. Independence not violated although there were different species with different spreads (this was to be expected since the spread is dependent on the number of overlaps for each).

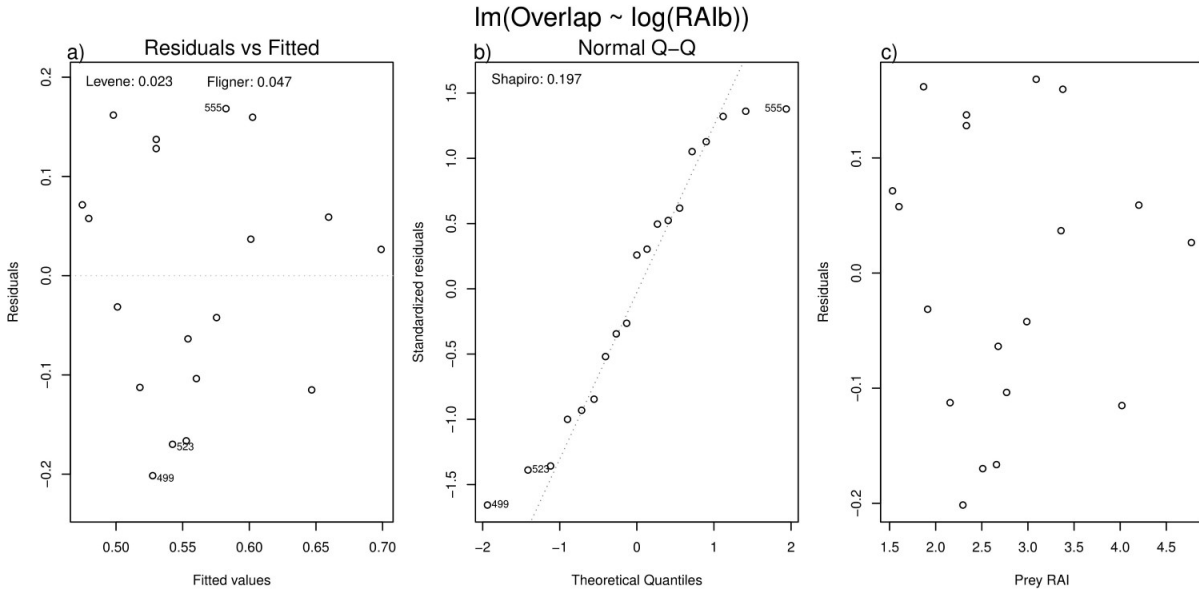**Coyote: Final Model -Prey RAI**

Figure 2: Model validation graphs for final model: Prey RAI. a) Fitted values versus residuals to assess homogeneity. There was variation in spread of residuals for each fitted value. The Levene p-value is signficant, as was the Fligner-Killeen p-value although close to the 0.5 alpha. b) QQnorm plot of residuals. Normality not violated with residuals close to normal line without any pattern and a Shapiro-Wilke p-value that was not signficant either. c) Residuals vs log(Prey RAIb). Independence not violated.

Coyote: Mass Advantage Linear Model (uses average Overlap)
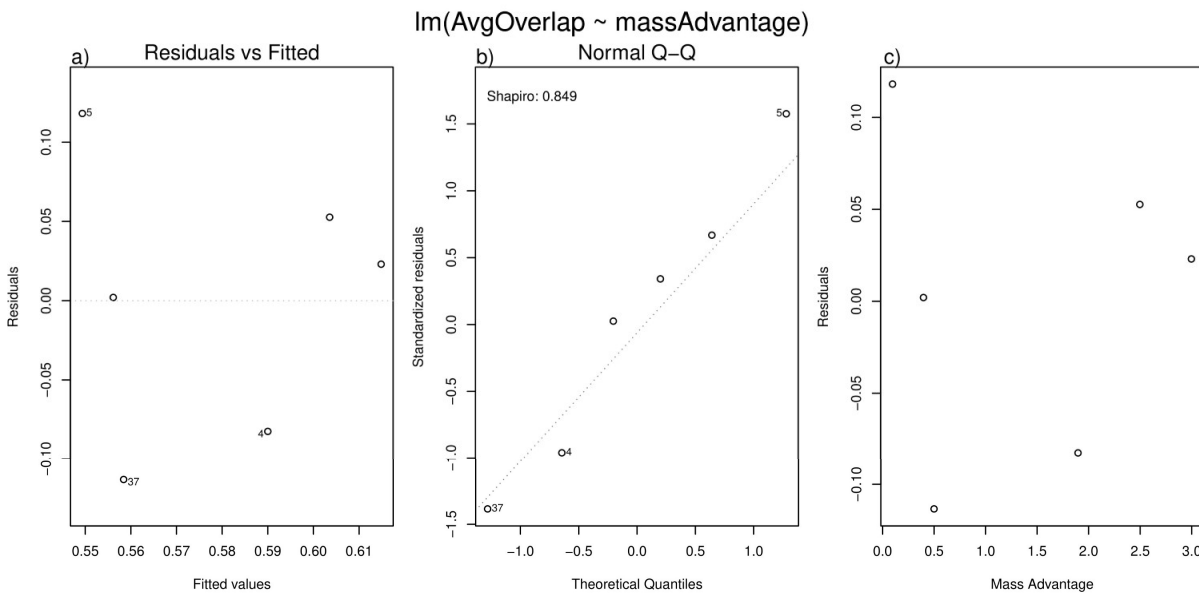

Figure 3: Model validation graphs for full model. a) Fitted values versus residuals to assess homogeneity. b) QQnorm plot of residuals. Normality not violated with residuals close to normal line without any pattern. Shapiro-Wilke p-value is not signficant either. c) Residuals vs Mass Advantage. Independence not violated.

Tests for homogeneity were unable to be run.

Ocelot

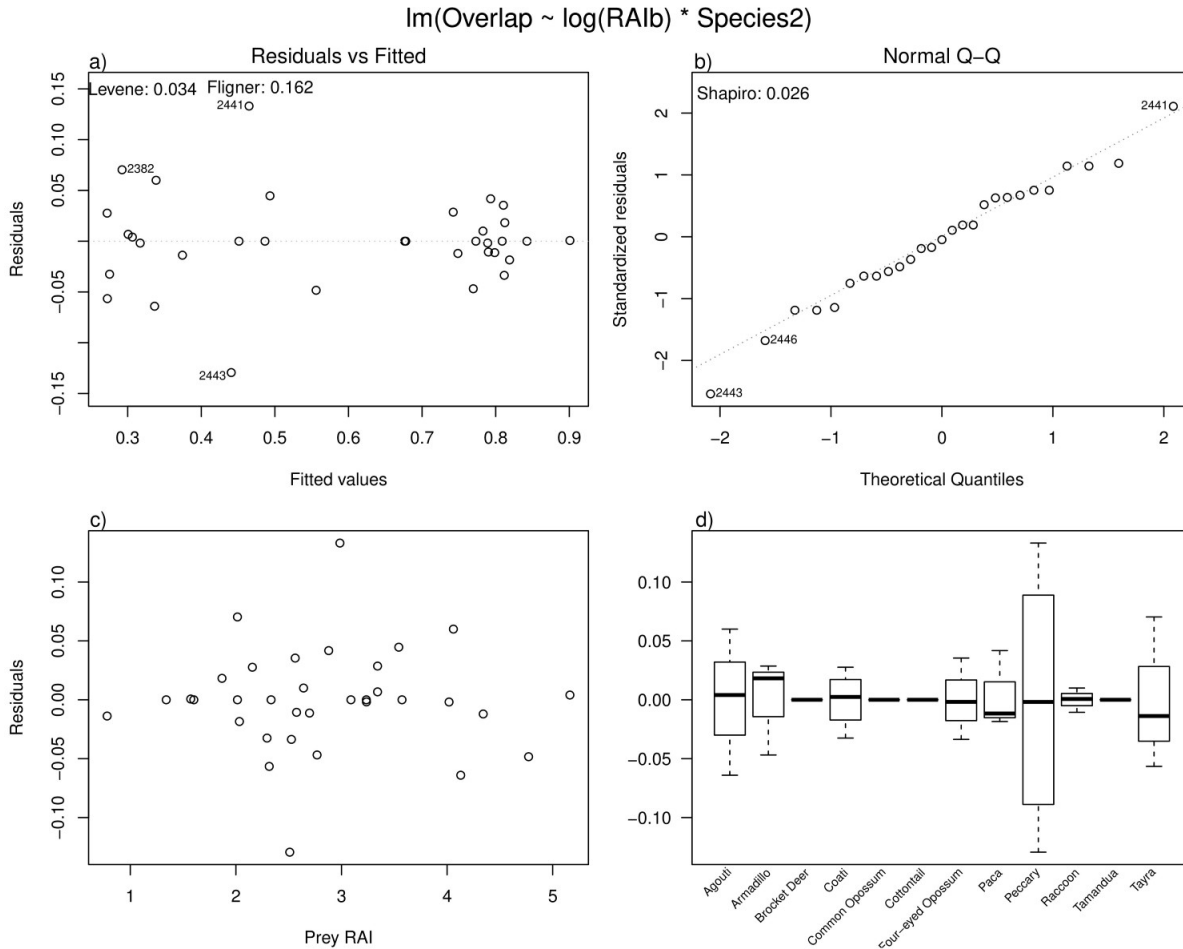### Ocelot: Full Model (lm(Overlap~log(Prey RAI)*Prey Species))

Figure 4: Model validation graphs for full model: Prey RAI * Prey Species. a) Fitted values versus residuals to assess homogeneity. There was minimal variation in spread of residuals for each fitted value. The Levene p-value was signficant, but the Fligner-Killeen p-value (more resistant to nonnormality) was not significant. b) QQnorm plot of residuals. Normality violated with residuals close to normal line but varied in a pattern. Shapiro-Wilke p-value was signficant. c) Residuals vs log(Prey RAIb). Independence not violated. d) Residuals versus prey species. Independence not violated although there were different species with different spreads (this was to be expected since the spread is dependent on the number of overlaps for each).
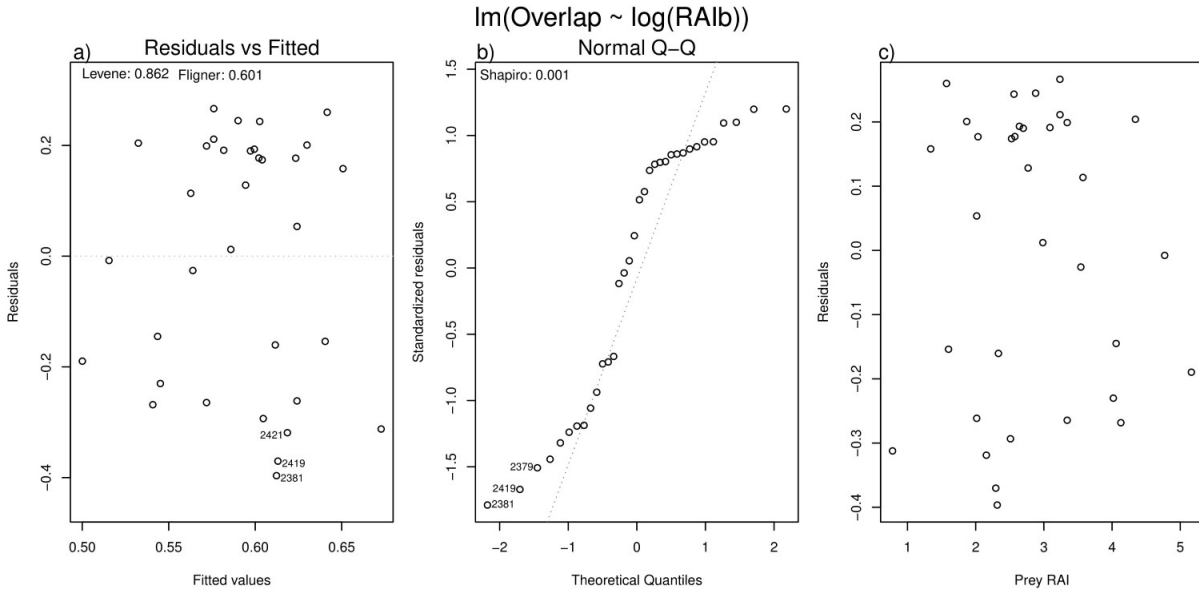

Ocelot: Prey RAI Model

Figure 5: Model validation graphs for model Prey RAI. a) Fitted values versus residuals to assess homogeneity. There was little variation in spread of residuals for each fitted value. The Levene p-value nor the Fligner-Killeen p-value were significant. b) QQnorm plot of residuals. Normality was violated with residuals that varied around the normal line in a pattern and a Shapiro-Wilke p-value that was significant. c) Residuals vs log(Prey RAIb). Independence not violated. *** ###Ocelot: Final Model -Prey Species
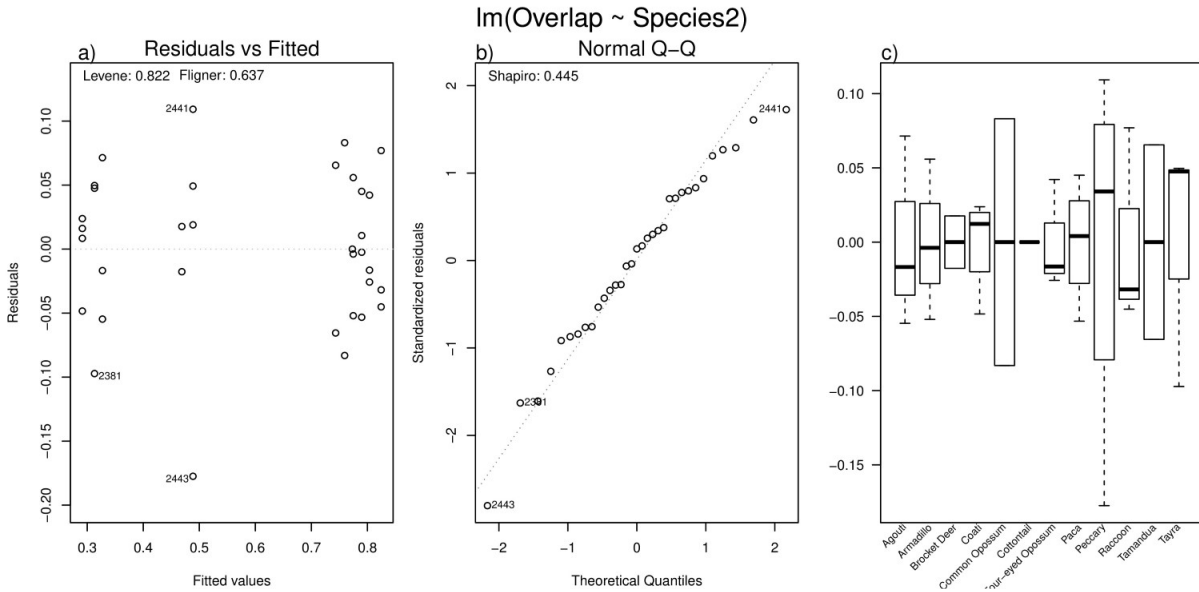

Figure 6: Model validation graphs for final model: Prey Species. a) Fitted values versus residuals to assess homogeneity. There was minimal variation in spread of residuals for each fitted value. Neither the Levene p-value nor the Fligner-Killeen p-value were significant. b) QQnorm plot of residuals. Normality not violated with residuals close to normal line without any pattern and a Shapiro-Wilke p-value that was not significant either. c) Residuals vs log(Prey RAIb). Independence not violated.

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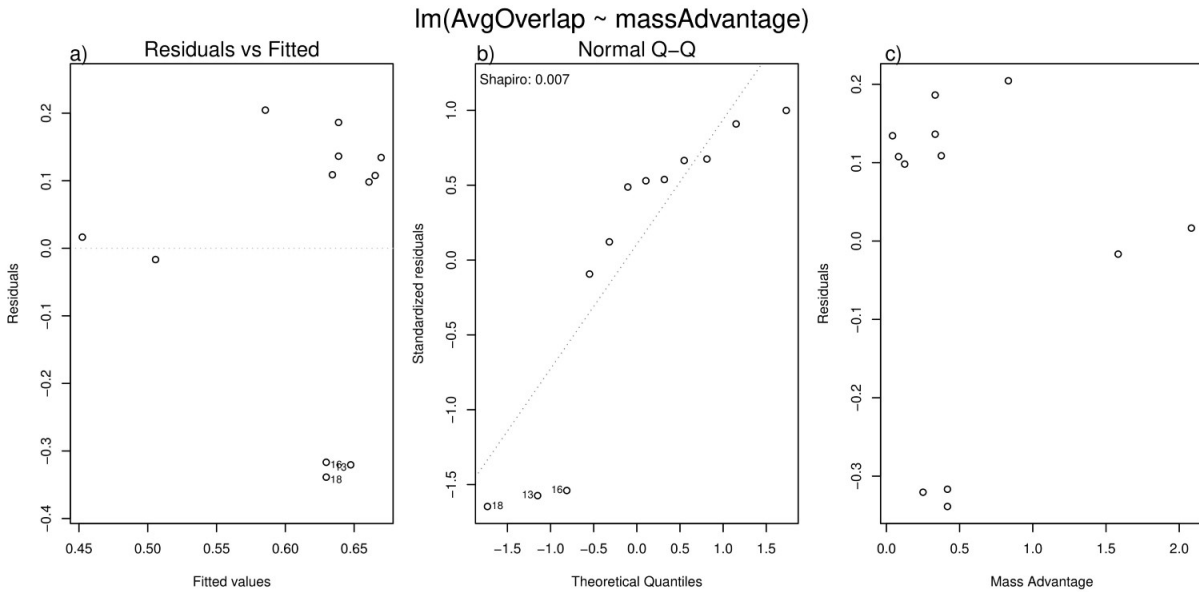**Ocelot: Mass Advantage Linear Model (uses average Overlap)**

Figure 7: Model validation graphs for mass advantage model. a) Fitted values versus residuals to assess homogeneity. Spread of residuals vary across fitted values. b) QQnorm plot of residuals. Normality violated with residuals varying significantly around normal in a pattern. Shapiro-Wilke p-value was signficant. c) Residuals vs Mass Advantage. Independence not violated.

Tests for homogeneity were unable to be run.

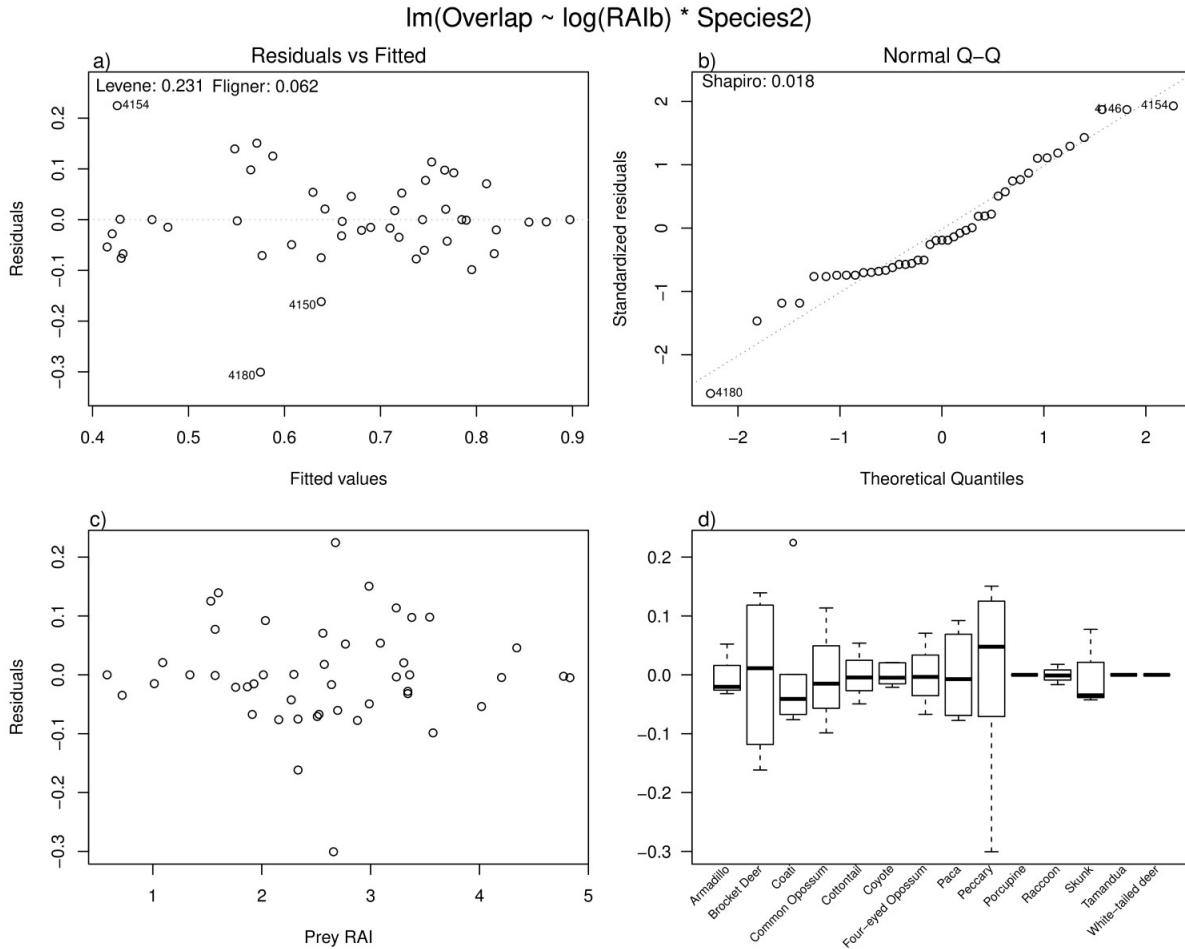**Puma: Full Model (lm(Overlap~log(Prey RAI)*Prey Species))**

Figure 8: Model validation graphs for full model: Prey RAI * Prey Species. a) Fitted values versus residuals to assess homogeneity. There was slight variation in spread of residuals for each fitted value. The Levene p-value and Fligner-Killeen p-value (more resistant to nonnormality) were not significant. b) QQnorm plot of residuals. Normality violated with residuals varying around normal with a distinct pattern. Shapiro-Wilke p-value was signficant. c) Residuals vs log(Prey RAIb). Independence not violated. d) Residuals versus prey species. Independence was not violated, although there were different species with different spreads (this was to be expected since the spread is dependent on the number of overlaps for each).

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Puma: Prey RAI Model

Figure 9: Model validation graphs for Prey RAI Model. a) Fitted values versus residuals to assess homogeneity. There was minimal variation in spread of residuals for each fitted value. The Levene p-value and the Fligner-Killeen p-value were not significant. b) QQnorm plot of residuals. Normality violated with residuals varying around normal in a pattern and a Shapiro-Wilke p-value that was signficant. c) Residuals vs log(Prey RAIb). Independence not violated.

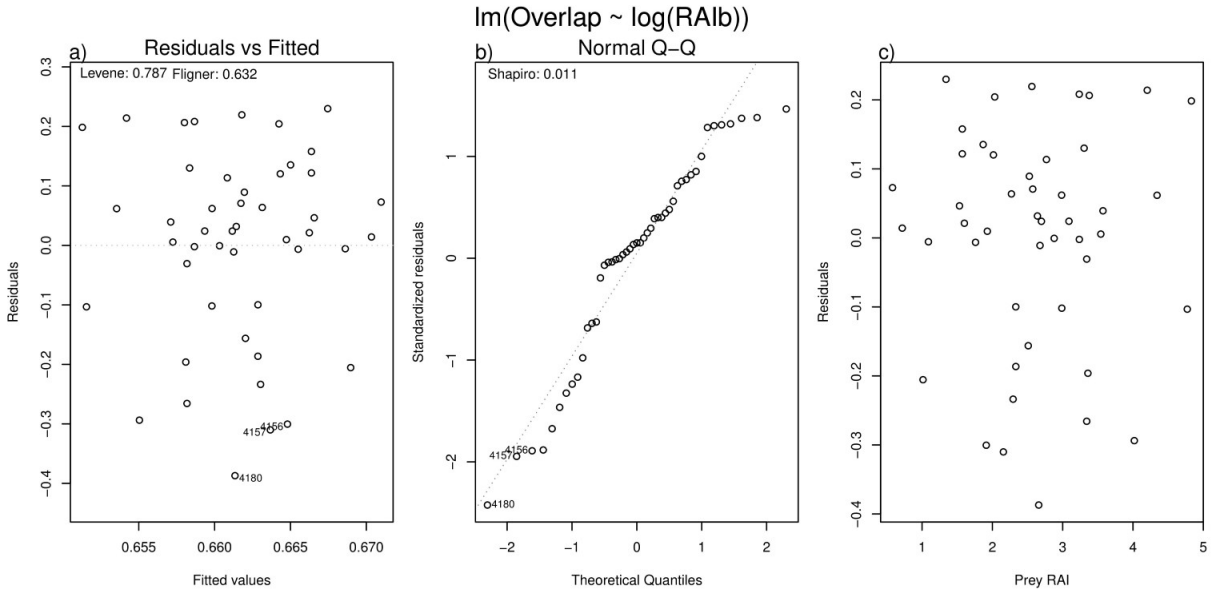**Puma: Prey Species Model**

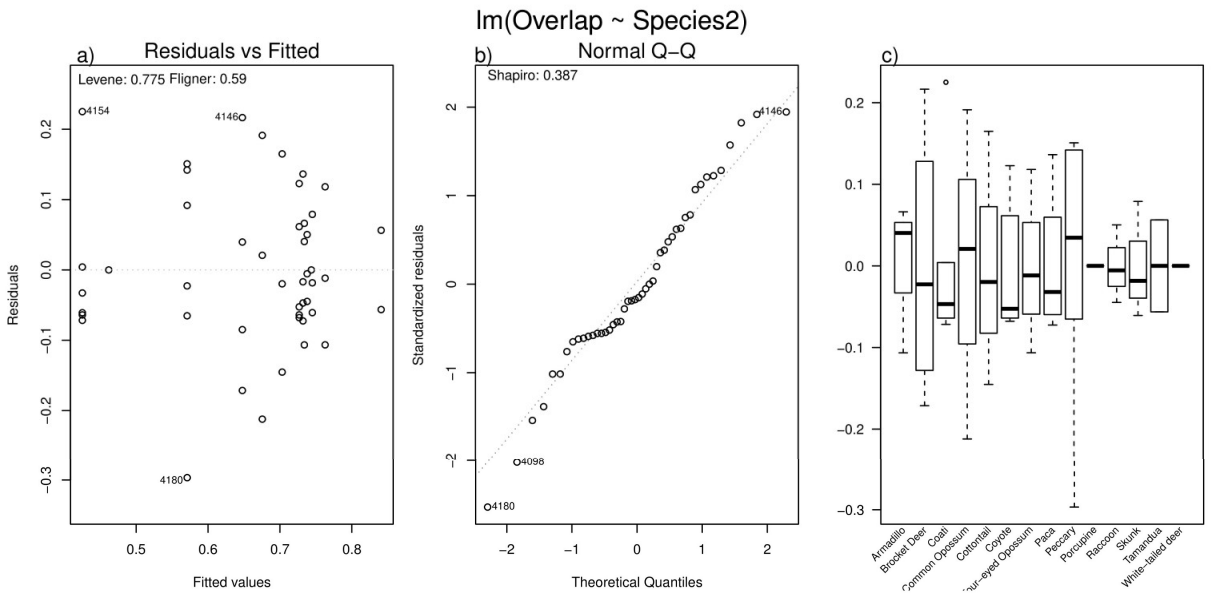Figure 10: Model validation graphs for Prey RAI Model. a) Fitted values versus residuals to assess homogeneity. There was minimal variation in spread of residuals for each fitted value. The Levene p-value and the Fligner-Killeen p-value were not significant. b) QQnorm plot of residuals. Normality was not violated with residuals close to the normal line and the Shapiro-Wilke p-value that was signficant. c) Residuals versus

prey species. Independence was not violated, although there were different species with different spreads (this was to be expected since the spread is dependent on the number of overlaps for each).

Puma: Mass Advantage Linear Model (uses average Overlap)

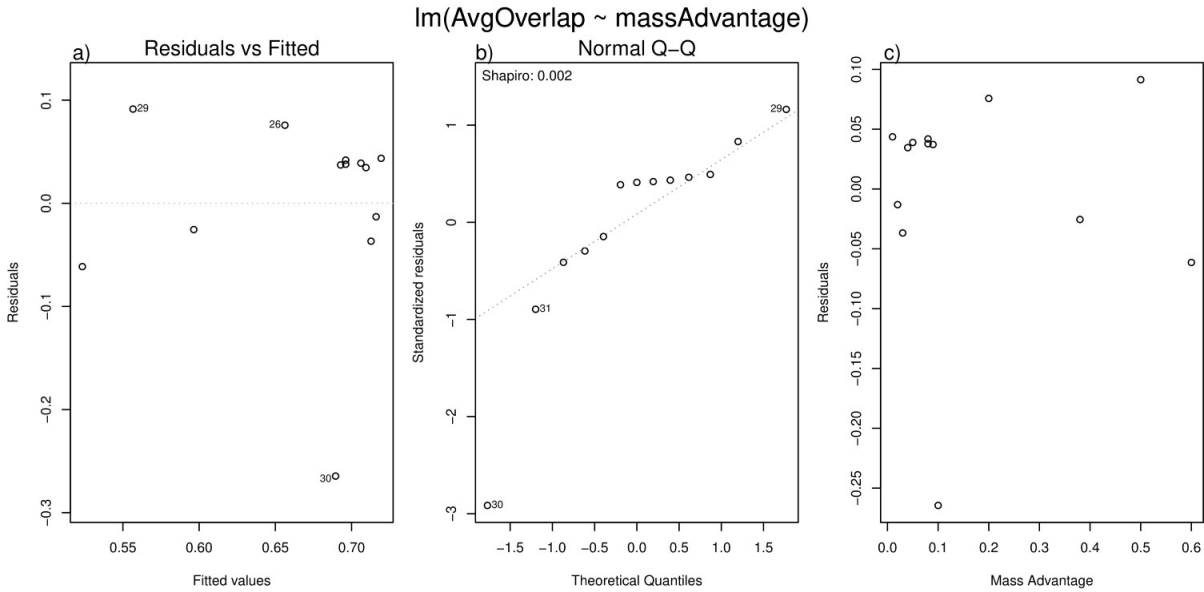Figure 11: Model validation graphs for full model. a) Fitted values versus residuals to assess homogeneity. Spread of residuals differed for fitted values b) QQnorm plot of residuals. Normality violated with residuals varying around normal with a distinct pattern. Shapiro-Wilke p-value was signficant. c) Residuals vs Mass Advantage. Independence not violated.

Tests for homogeneity were unable to be run.

Appendix B: RAI and Coefficient of Overlapping at Each Site

Table 1: Coyote by Prey Species

	Site	Prey Species	n	RAI	Coef of Overlapping
1	ASBC	Armadillo	39	6.478	0.660
2	Cabo Blanco	Armadillo	51	15.938	0.457
3	Tapanti	Brocket Deer	266	29.311	0.762
4	Savegre	Brocket Deer	75	4.962	0.537
5	Chirripo	Brocket Deer	70	10.306	0.658
6	Cabo Blanco	Brocket Deer	33	10.312	0.668
7	Tapanti	Coati	132	14.545	0.490
8	Savegre	Coati	150	9.923	0.326
9	Chirripo	Coati	46	6.773	0.470
10	ASBC	Coati	52	8.638	0.405
11	Cabo Blanco	Coati	178	55.625	0.532
17	Tapanti	Cottontail	180	19.835	0.533
18	Savegre	Cottontail	332	21.963	0.751
19	Chirripo	Cottontail	454	66.843	0.718
13	Tapanti	Peccary	42	4.628	0.546
14	Savegre	Peccary	186	12.305	0.372
15	Chirripo	Peccary	97	14.282	0.386
16	Cabo Blanco	Peccary	378	118.125	0.725
12	Cabo Blanco	White-tailed deer	92	28.750	0.638

Table 2: Coyote by Site

	Site	Prey Species	n	RAI	Coef of Overlapping
1	ASBC	Armadillo	39	6.478	0.660
10	ASBC	Coati	52	8.638	0.405
2	Cabo Blanco	Armadillo	51	15.938	0.457
6	Cabo Blanco	Brocket Deer	33	10.312	0.668
11	Cabo Blanco	Coati	178	55.625	0.532
12	Cabo Blanco	White-tailed deer	92	28.750	0.638
16	Cabo Blanco	Peccary	378	118.125	0.725
5	Chirripo	Brocket Deer	70	10.306	0.658
9	Chirripo	Coati	46	6.773	0.470
15	Chirripo	Peccary	97	14.282	0.386
19	Chirripo	Cottontail	454	66.843	0.718
4	Savegre	Brocket Deer	75	4.962	0.537
8	Savegre	Coati	150	9.923	0.326
14	Savegre	Peccary	186	12.305	0.372
18	Savegre	Cottontail	332	21.963	0.751
3	Tapanti	Brocket Deer	266	29.311	0.762
7	Tapanti	Coati	132	14.545	0.490
13	Tapanti	Peccary	42	4.628	0.546
17	Tapanti	Cottontail	180	19.835	0.533

Table 3: Ocelot by Prey Species

	Site	Prey Species	n	RAI	Coef of Overlapping
5	Marta, Copal	Agouti	82	57.951	0.399
6	ASBC	Agouti	374	62.126	0.272
7	Cabo Blanco	Agouti	559	174.688	0.310
8	Marta, Copal	Armadillo	40	28.269	0.771
9	ASBC	Armadillo	39	6.478	0.831
10	Cabo Blanco	Armadillo	51	15.938	0.723
16	Savegre	Brocket Deer	75	4.962	0.486
17	Cabo Blanco	Brocket Deer	33	10.312	0.451
18	Marta, Copal	Coati	40	28.269	0.307
19	Savegre	Coati	150	9.923	0.243
20	ASBC	Coati	52	8.638	0.300
21	Cabo Blanco	Coati	178	55.625	0.315
11	ASBC	Common Opossum	153	25.415	0.842
12	Cabo Blanco	Common Opossum	114	35.625	0.676
31	Savegre	Cottontail	332	21.963	0.773
25	Marta, Copal	Four-eyed Opossum	36	25.442	0.787
26	ASBC	Four-eyed Opossum	78	12.957	0.846
27	Cabo Blanco	Four-eyed Opossum	40	12.500	0.778
1	Marta, Copal	Paca	21	14.841	0.787
2	Savegre	Paca	269	17.796	0.835
3	ASBC	Paca	46	7.641	0.800
4	Cabo Blanco	Paca	246	76.875	0.737
22	Marta, Copal	Peccary	28	19.788	0.598
23	Savegre	Peccary	186	12.305	0.311
24	Cabo Blanco	Peccary	378	118.125	0.508
28	Savegre	Raccoon	212	14.025	0.793
29	ASBC	Raccoon	29	4.817	0.902
30	Cabo Blanco	Raccoon	42	13.125	0.779
32	ASBC	Tamandua	23	3.821	0.809
33	Cabo Blanco	Tamandua	24	7.500	0.678
13	Savegre	Tayra	33	2.183	0.361
14	ASBC	Tayra	61	10.133	0.216
15	Cabo Blanco	Tayra	24	7.500	0.363

Table 4: Ocelot by Site

	Site	Prey Species	n	RAI	Coef of Overlapping
3	ASBC	Paca	46	7.641	0.800
6	ASBC	Agouti	374	62.126	0.272
9	ASBC	Armadillo	39	6.478	0.831
11	ASBC	Common Opossum	153	25.415	0.842
14	ASBC	Tayra	61	10.133	0.216
20	ASBC	Coati	52	8.638	0.300
26	ASBC	Four-eyed Opossum	78	12.957	0.846
29	ASBC	Raccoon	29	4.817	0.902
32	ASBC	Tamandua	23	3.821	0.809
4	Cabo Blanco	Paca	246	76.875	0.737
7	Cabo Blanco	Agouti	559	174.688	0.310
10	Cabo Blanco	Armadillo	51	15.938	0.723
12	Cabo Blanco	Common Opossum	114	35.625	0.676
15	Cabo Blanco	Tayra	24	7.500	0.363
17	Cabo Blanco	Brocket Deer	33	10.312	0.451
21	Cabo Blanco	Coati	178	55.625	0.315
24	Cabo Blanco	Peccary	378	118.125	0.508
27	Cabo Blanco	Four-eyed Opossum	40	12.500	0.778
30	Cabo Blanco	Raccoon	42	13.125	0.779
33	Cabo Blanco	Tamandua	24	7.500	0.678
1	Marta, Copal	Paca	21	14.841	0.787
5	Marta, Copal	Agouti	82	57.951	0.399
8	Marta, Copal	Armadillo	40	28.269	0.771
18	Marta, Copal	Coati	40	28.269	0.307
22	Marta, Copal	Peccary	28	19.788	0.598
25	Marta, Copal	Four-eyed Opossum	36	25.442	0.787
2	Savegre	Paca	269	17.796	0.835
13	Savegre	Tayra	33	2.183	0.361
16	Savegre	Brocket Deer	75	4.962	0.486
19	Savegre	Coati	150	9.923	0.243
23	Savegre	Peccary	186	12.305	0.311
28	Savegre	Raccoon	212	14.025	0.793
31	Savegre	Cottontail	332	21.963	0.773

Table 5: Puma by Prey Species

	Site	Prey Species	n	RAI	Coef of Overlapping
14	Marta, Copal	Armadillo	40	28.269	0.628
15	ASBC	Armadillo	39	6.478	0.800
16	Cabo Blanco	Armadillo	51	15.938	0.774
20	Tapanti	Brocket Deer	266	29.311	0.864
21	Savegre	Brocket Deer	75	4.962	0.688
22	Chirripo	Brocket Deer	70	10.306	0.563
23	Cabo Blanco	Brocket Deer	33	10.312	0.476
24	Marta, Copal	Coati	40	28.269	0.392
25	Tapanti	Coati	132	14.545	0.650
26	Savegre	Coati	150	9.923	0.429
27	Chirripo	Coati	46	6.773	0.364
28	ASBC	Coati	52	8.638	0.354
29	Cabo Blanco	Coati	178	55.625	0.361
17	Tapanti	Common Opossum	25	2.755	0.464
18	ASBC	Common Opossum	153	25.415	0.867
19	Cabo Blanco	Common Opossum	114	35.625	0.696
42	Tapanti	Cottontail	180	19.835	0.558
43	Savegre	Cottontail	332	21.963	0.684
44	Chirripo	Cottontail	454	66.843	0.868
1	Tapanti	Coyote	27	2.975	0.663
2	Savegre	Coyote	1,893	125.232	0.850
3	Chirripo	Coyote	185	27.238	0.788
4	ASBC	Coyote	35	5.814	0.659
5	Cabo Blanco	Coyote	22	6.875	0.674
36	Marta, Copal	Four-eyed Opossum	36	25.442	0.656
37	ASBC	Four-eyed Opossum	78	12.957	0.881
38	Cabo Blanco	Four-eyed Opossum	40	12.500	0.751
10	Marta, Copal	Paca	21	14.841	0.685
11	Savegre	Paca	269	17.796	0.660
12	ASBC	Paca	46	7.641	0.868
13	Cabo Blanco	Paca	246	76.875	0.715
31	Marta, Copal	Peccary	28	19.788	0.722
32	Tapanti	Peccary	42	4.628	0.713
33	Savegre	Peccary	186	12.305	0.506
34	Chirripo	Peccary	97	14.282	0.274
35	Cabo Blanco	Peccary	378	118.125	0.548
6	Savegre	Porcupine	27	1.786	0.744
39	Savegre	Raccoon	212	14.025	0.693
40	ASBC	Raccoon	29	4.817	0.788
41	Cabo Blanco	Raccoon	42	13.125	0.732
7	Savegre	Skunk	31	2.051	0.684
8	ASBC	Skunk	29	4.817	0.824
9	Cabo Blanco	Skunk	31	9.688	0.727
45	ASBC	Tamandua	23	3.821	0.897
46	Cabo Blanco	Tamandua	24	7.500	0.785
30	Cabo Blanco	White-tailed deer	92	28.750	0.462

Table 6: Puma by Site

	Site	Prey Species	n	RAI	Coef of Overlapping
4	ASBC	Coyote	35	5.814	0.659
8	ASBC	Skunk	29	4.817	0.824
12	ASBC	Paca	46	7.641	0.868
15	ASBC	Armadillo	39	6.478	0.800
18	ASBC	Common Opossum	153	25.415	0.867
28	ASBC	Coati	52	8.638	0.354
37	ASBC	Four-eyed Opossum	78	12.957	0.881
40	ASBC	Raccoon	29	4.817	0.788
45	ASBC	Tamandua	23	3.821	0.897
5	Cabo Blanco	Coyote	22	6.875	0.674
9	Cabo Blanco	Skunk	31	9.688	0.727
13	Cabo Blanco	Paca	246	76.875	0.715
16	Cabo Blanco	Armadillo	51	15.938	0.774
19	Cabo Blanco	Common Opossum	114	35.625	0.696
23	Cabo Blanco	Brocket Deer	33	10.312	0.476
29	Cabo Blanco	Coati	178	55.625	0.361
30	Cabo Blanco	White-tailed deer	92	28.750	0.462
35	Cabo Blanco	Peccary	378	118.125	0.548
38	Cabo Blanco	Four-eyed Opossum	40	12.500	0.751
41	Cabo Blanco	Raccoon	42	13.125	0.732
46	Cabo Blanco	Tamandua	24	7.500	0.785
3	Chirripo	Coyote	185	27.238	0.788
22	Chirripo	Brocket Deer	70	10.306	0.563
27	Chirripo	Coati	46	6.773	0.364
34	Chirripo	Peccary	97	14.282	0.274
44	Chirripo	Cottontail	454	66.843	0.868
10	Marta, Copal	Paca	21	14.841	0.685
14	Marta, Copal	Armadillo	40	28.269	0.628
24	Marta, Copal	Coati	40	28.269	0.392
31	Marta, Copal	Peccary	28	19.788	0.722
36	Marta, Copal	Four-eyed Opossum	36	25.442	0.656
2	Savegre	Coyote	1,893	125.232	0.850
6	Savegre	Porcupine	27	1.786	0.744
7	Savegre	Skunk	31	2.051	0.684
11	Savegre	Paca	269	17.796	0.660
21	Savegre	Brocket Deer	75	4.962	0.688
26	Savegre	Coati	150	9.923	0.429
33	Savegre	Peccary	186	12.305	0.506
39	Savegre	Raccoon	212	14.025	0.693
43	Savegre	Cottontail	332	21.963	0.684
1	Tapanti	Coyote	27	2.975	0.663
17	Tapanti	Common Opossum	25	2.755	0.464
20	Tapanti	Brocket Deer	266	29.311	0.864
25	Tapanti	Coati	132	14.545	0.650
32	Tapanti	Peccary	42	4.628	0.713
42	Tapanti	Cottontail	180	19.835	0.558

Appendix C: Camera Data

Site	Survey	*Number Cameras	Camera Days	Start Date	End Date	Latitude	Longitude	Elevation (m)	Elevation Type
ASBC	Alexander Skutch Biological Corridor (CoBAS)	4-18	3077	7/3/2012	3/30/2015	9.5633	-83.7839	338-888	Lowland
	Bosque de Agua Biological Corridor (CoBBA)	8	617	6/21/2016	#########	9.265	-83.421	851-1672	Low/ Midland
	Los Cusingos Bird Sanctuary (LCBS)	2-4	2326	7/3/2012	2/28/2015	9.3367	-83.6287	724-727	Lowland
Cabo Blanco	Cabo Blanco National Park (PNCB)	6	868	7/17/2015	9/20/2016	9.582	-85.101	63-321	Lowland
	La Cangreja National Park (PNLC)		2071			9.7034	-184.3979	338-584	Lowland
	Carara National Park (PNC)	3		9/26/2014	8/9/2015	9.7984	-84.5979	28-64	Lowland
Chirripo	Chirripo National Park (PNCH)	2-22	6792	6/26/2012	6/2/2017	9.4599	-83.5619	2308-3464	Highland
Marta, Copal	La Marta National Wildlife Refuge	2-4	766	7/20/2013	4/26/2015	9.7685	-83.6823	747-1003	Lowland/Midland
	El Copal Private Reserve (ECR)	4	649	1/8/2013	9/17/2016	9.7804	-83.7546	1158-1225	Midland
PILA	La Amistad International Park (PILA)	5	1396	5/30/2017	2/2/2018	9.0539	-82.9876	2086-2308	Highland
Tapanti	Tapantí Macizo de la Muerte National Park (PNTMM)	4-14	9075	6/18/2012	#########	9.7068	-83.7793	1506-2803	Mid/ Highland
Savegre	Los Quetzales National Park (PNLQ)	1-12	5963	6/19/2013	6/5/2017	9.5594	-83.7872	2569-3118	Highland
	Savegre Lodge Private Reserve (SLPR)	5-15	9153	6/29/2010	6/7/2017	9.5502	-83.7911	2112-3118	Highland

* The range of the number of cameras deployed at any one time.