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Group dynamics, behavior, and current and historical abundance of peccaries in Costa Rica's Caribbean lowlands

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The abundances and habitat preferences of peccaries in Neotropical forests are important to understand because these keystone species influence many aspects of the ecosystem. In the Caribbean lowlands of Costa Rica, we conducted walking surveys for ~2 years to study the behavior and population trends of collared peccaries (*Pecari tajacu*), and found that peccaries are abundant at La Selva Biological Station and overall, detection rates were relatively constant through time. A stable estimate of detection rates was achieved only after 7–9 months of surveying. We found no habitat preferences between primary and secondary forest, yet there were some differences in group dynamics—group radius was larger and sighting distance was greater in primary forest, whereas the number of singletons was higher in secondary forest. More peccaries were seen closer to the laboratory clearing than at greater distances, for a variety of probable reasons: habituation to humans, lower predation and hunting pressure, and various environmental and habitat factors. Peccary groups had spatially clumped distributions across the landscape and were more active diurnally than nocturnally. Collared peccary densities are relatively high at La Selva compared to other Neotropical sites, with the exception of Barro Colorado Island. We combined our data with a review of the historical literature to assess changes in the populations of peccaries in the Caribbean lowlands. We found that collared peccaries have likely increased in abundance at La Selva, seemingly a few years after the extirpation of white-lipped peccaries (*Tayassu pecari*), which were abundant in the area 40–50 years ago. An understanding of the group dynamics, behavior, and habitat preference of collared peccaries is essential for management decisions and conservation efforts. Additionally, assessment of population changes should be carefully considered in a historical context, with a particular focus on how the populations of the 2 peccary species have changed, and how these species might differentially affect their environment.

Key words: Central America, detection rates, *Pecari tajacu*, strip-census techniques, *Tayassu pecari*

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Ungulates can have large impacts on ecosystems, affecting nutrient cycling and the composition of plant and animal communities (Bodmer 1991; Hobbs 1996; Augustine and McNaughton 1998; Cullen et al. 2001; Rooney and Waller 2003). The manner and extent to which ungulate populations respond to environmental changes are complex, not easy to discern, and often species-specific (Laurance et al. 2008; van Beest et al. 2012). Ungulate populations worldwide are susceptible to anthropogenic disturbances (Peres 2001; Laliberte and Ripple 2004). In the Neotropics, where ecosystems are experiencing major faunal changes (Daily et al. 2003; Sigel et al. 2006; Whitfield et al. 2007), historical and current data for most ungulate species are lacking. An example is the abundance of 2 peccary species, the white-lipped peccary (*Tayassu pecari*) and the collared peccary (*Pecari tajacu*) of the Caribbean lowlands of Costa Rica.

Peccaries are ecologically important because they act as ecosystem engineers (Keuroghlian and Eaton 2009; Beck et al. 2010), modify plant diversity and composition by trampling seedlings (Beck 2007), and act as seed predators (Bodmer 1991; Beck and Terborgh 2002; Kuprewicz and García-Robledo 2010) and seed dispersers (Beck 2006; Keuroghlian

and Eaton 2009; Lazure et al. 2010). Peccaries consume a wide variety of food items throughout their range, but in the tropics they primarily eat fruits, seeds (especially palms), pulp, roots, tubers, and occasionally animals (Kiltie 1981; Olmos 1993; Barreto et al. 1997; Altrichter et al. 2001; Beck 2006). Additionally, peccaries are important prey items for large carnivores, especially jaguars (*Panthera onca*) and pumas (*Puma concolor*—Harveson et al. 2000; Garla et al. 2001; Novack et al. 2005; Weckel et al. 2006a, 2006b).

Historically, collared and white-lipped peccaries shared much of their ranges; however, white-lipped peccaries have suffered severe population declines due to anthropogenic factors, especially overhunting (Peres 1996; Chiarello 1999; Cullen et al. 2000). Collared peccaries also are susceptible to human disturbances, although they are more resilient than white-lipped peccaries (Cullen et al. 2000; Altrichter and Boaglio 2004). Both peccary species represent a large proportion and biomass of hunted animals throughout their ranges (De Souza-Mazurek et al. 2000; Wright et al. 2000; Roldán and Simonetti 2001; Bonaudo et al. 2005). In areas where collared and white-lipped peccaries co-occur, white-lipped peccaries may outcompete collared peccaries (Altrichter and Boaglio 2004; Keuroghlian et al. 2004; Mendes Pontes and Chivers 2007). Although behavioral and morphological differences cause niche differentiation between these species (Kiltie 1982; Desbiez et al. 2009), ecologically the 2 species probably have similar impacts on forests.

Peccaries present interesting challenges as study subjects. Standard methods to estimate population densities are difficult to apply because it is difficult to determine group size, and individuals have no unique identifying markings. Estimating densities is particularly complicated in tropical, nondeciduous forests, where a dense understory reduces visibility.

Although much research has been done on peccaries, many aspects of their ecology in the tropics are still poorly understood. The biology of collared peccaries in the tropics is not the same as in arid areas because of well-known dietary and behavioral differences. In particular, there are few data on peccaries in the Caribbean lowlands of Central America. Peccaries in this area have suffered from increased hunting pressure and habitat change, as in many other areas of the Neotropics. White-lipped peccaries still persist in remote areas of the Caribbean lowlands, but have been locally extirpated from the majority of their historical range. In Costa Rica's Caribbean lowlands, La Selva Biological Station (hereafter, La Selva) provides an excellent opportunity to study collared peccaries. At La Selva, collared peccaries are commonly observed, are relatively well protected, and have become a species of broad interest to scientists, local residents, ecotourists, and educators. Collared peccaries are generally perceived to have increased in density in recent years, to the extent that they may be negatively impacting the forest (Michel and Sherry 2012). A debate about managing peccary populations has arisen, but few historical data exist to assess long-term changes quantitatively.

We have observed and surveyed collared peccaries at La Selva for a number of years and herein combine our data with a review of the historical literature to form a broader picture of peccary biology and impact in the Caribbean lowlands. The aims of this paper are to elucidate population trends and detection rates of collared peccaries during a 2-year period, evaluate the efficacy of sampling via line transects, understand behavior and group dynamics of collared peccaries, and describe population estimates over space and time for collared and white-lipped peccaries. We will explore these themes by asking the following questions: What are the detection rates of peccaries and what do these rates inform us about population trends? How do survey methodologies affect peccary detection rates? What environmental factors affect the detection rate of peccaries? How do habitat type, time of day, and distance from the laboratory clearing (developed area that includes laboratory buildings and housing; hereafter, lab clearing) affect peccary group dynamics and behavior? How are peccaries distributed across the landscape? What are current population estimates? What were the historical abundances of collared and white-lipped peccaries?

Materials and Methods

Study area and data collection.—We conducted mammal surveys at Estación Biológica La Selva in the Caribbean lowlands of northeastern Costa Rica (10°26′N, 83°59′W). La Selva, which is connected to Parque Nacional Braulio Carrillo (~480 km^2), is composed of primary forest, selectively logged primary forest, successional secondary forests, and abandoned pastures and plantations, totaling just over 16 km^2 (McDade and Hartshorn 1994). Annual average rainfall is ~4 m, with precipitation peaks occurring in June–August and October–November (Clark and Clark 2010; McClearn et al., in press). La Selva is a well-protected site with professional park guards patrolling the property. Still, guards find evidence of illegal hunting and encounter hunters on occasion. The mammalian fauna of La Selva is typical of Neotropical rain forests and the majority of species are of widespread distribution (Timm 1994).

We walked 5 preexisting trails on 348 survey days between September 2005 and June 2007, traversing primary forest, different types of secondary forest, managed successional areas, the arboretum, and the ecological reserve (Fig. 1). We walked 4 trails (trails 1–4) diurnally and 1 trail (trail 5) nocturnally, starting at ~0700 h and 1900 h, respectively. In the event of heavy rainfall during a survey, the observer paused until conditions improved, or abandoned the survey if it could not be completed by 1100 h or 2300 h. We employed powerful flashlights during night surveys to detect and identify animals. Throughout the survey, some trails occasionally were walked in the opposite direction. Trails were not of equal length, but we walked a total of 1,052.36 km (848.36 km diurnally and 204 km nocturnally), totaling 981.7 h.

During our survey, we walked at ~1 km/h searching for collared peccaries and other mammals, and recorded the

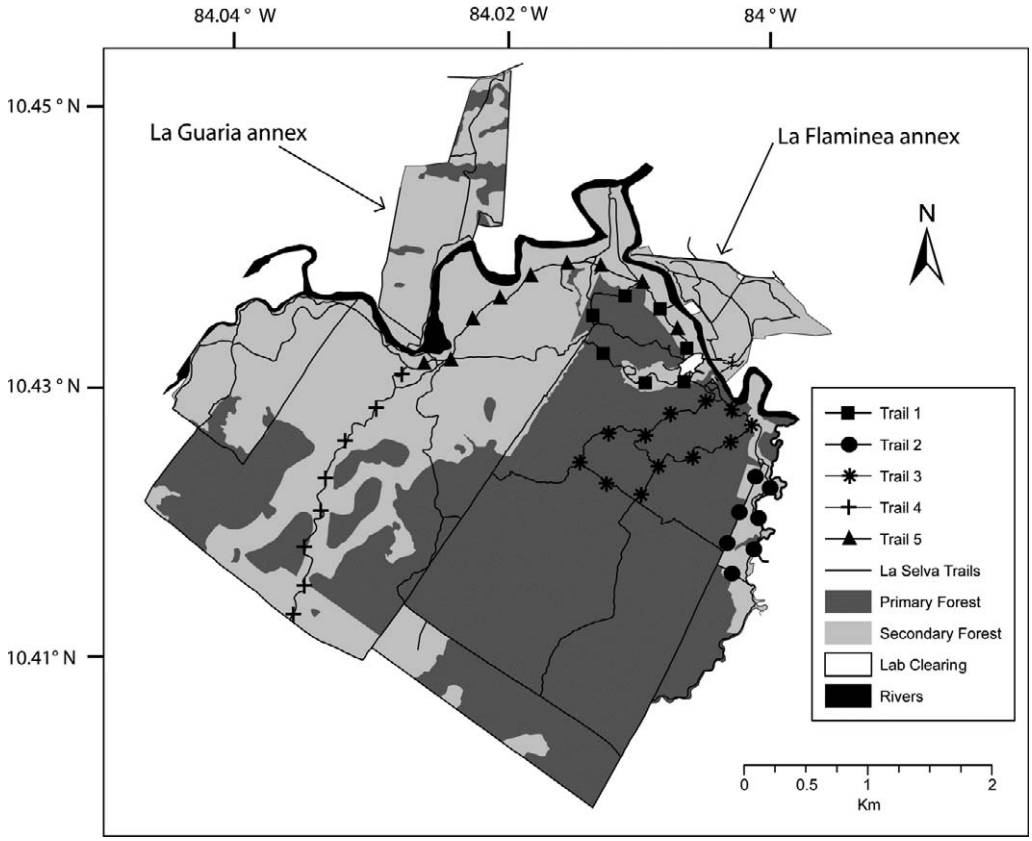

Fig. 1.—Map of La Selva Biological Station, Sarapiquí, Costa Rica. Trails 1–4 were walked diurnally and trail 5 was walked nocturnally for this study.

following variables: time of sighting, location of sighting, perpendicular distance from 1st observed animal to the trail, number of individuals, radius of group, and whether the animal was 1st detected by sight or hearing. We recorded peccary groups as 1 encounter. All distances were visually estimated. Only 1 observer walked the trails, except during the last 5 months of the survey, when 2 observers walked the diurnal portions of the survey together. During analysis, we estimated the perpendicular distance from the trail such that animals within that distance were certain to be observed (i.e., the detection rate started to drop at that distance).

Detection rates.—Detection rates were calculated in 2 manners: the number of encounters per hour walked (DRHr) and the number of encounters per kilometer walked (DRKm). The 2 rates (DRHr and DRKm) were correlated to test if they were interchangeable. We used a chi-square test, with expected values standardized by kilometers walked diurnally and nocturnally, to test for activity differences during day and nighttime. We used diurnal data throughout this study, unless specified, because peccaries are not as active nocturnally.

To test for biases in detection rate due to increased sampling effort during the last 5 months of the survey, we used analysis of covariance, because rainfall in this seasonal environment was found to be marginally significant. We omitted data from January 2007 because in this month the number of observers increased to 2.

The observer recorded if detection was based on sight (visual detection) or sound (vocalizations or noises created by movement in the environment). To determine if peccaries were detected more by sight or sound, we performed a chi-square goodness-of-fit test.

We plotted monthly DRKm through time to observe population trends. Because monthly DRKm varied widely through time, we explored the amount of sampling effort needed to find a stable DRKm estimate. We randomized the order of the daily data (number of peccary sightings and kilometers walked) over 100 iterations and calculated a cumulative daily DRKm. We then found the amount of effort such that 95% of the cumulative daily DRKm stabilized within $\pm 10\%$ and $\pm 5\%$ of the total DRKm.

Although our data initially appear to be suited for distance sampling (Buckland et al. 2001), several assumptions of the procedures are not met, rendering this method unsuitable. First, the "shape criterion," wherein the detection function should have a shoulder, implying that "detectability is certain near the line or point and stays certain or nearly certain for some distance" (Buckland et al. 2001:36), is not observed in our data. A histogram of perpendicular sighting distances shows a high proportion of sightings within 1 m from the trail, and a drastic reduction thereafter. Second, a spike in sightings closer to the trail, and differences in the perpendicular sighting distances in different forest types, suggest that peccaries are not

uniformly distributed with respect to perpendicular distance from the line. Finally, the strong effect of the lab clearing on detection rates indicates that peccaries are not distributed in the area according to some stochastic process. Examination of our peccary data highlights several pitfalls that may be associated with line transect sampling, particularly in meeting the assumptions of the tests.

Environmental factors.—To test whether mean daily rainfall (mm), air temperature (°C), minimum air temperature (°C), and maximum air temperature (°C) of the current or previous month, or both, were associated with monthly DRHr, we performed a stepwise linear regression with alpha-to-enter and alpha-to-remove equal to 0.15. We calculated the values for these environmental factors from the meteorological weather stations of the Organization for Tropical Studies at La Selva (Organization for Tropical Studies 2011a).

Primary and secondary forest effects.—We categorized each peccary sighting by forest type (primary versus secondary) by using geographic information system land-use layers from the Organization for Tropical Studies La Selva Geographic Information Systems Web site (Organization for Tropical Studies 2011b). Primary forest included primary forest and ecological reserves, and secondary forest included all secondary forest types.

We used a chi-square test, with expected values standardized by kilometers walked in each forest type, to assess preference for primary or secondary forest. We tested whether group size, group radius, and perpendicular sighting distance from the trail were different in primary versus secondary forest. Group sizes, group radii, and sighting distances were not normally distributed; consequently, we used Mann–Whitney *U*-tests. We used a contingency table and a chi-square test with Yate's correction to test if the proportion of singletons in primary and secondary forest differed. Observer ability to visually detect a peccary in both primary and secondary forest was estimated in the field and distances were measured.

Diurnal and nocturnal differences.—We tested whether group size, group radius, and perpendicular sighting distance were different for peccaries sighted diurnally and nocturnally by using Mann–Whitney *U*-tests.

Effect of lab clearing.—To determine whether distance from the lab clearing affected peccary sightings, for groups and total number of individuals seen, data were entered into a geospatial framework using ArcMap 10 (ESRI, Inc. 2010). We created incremental rings of 300 m around the edge of the lab clearing and found detection rates (group DRKm and total number of individuals DRKm) for each transect within each ring. We regressed detection rates onto the distance from the lab clearing using the middle distance of each ring as the value for the independent variable (i.e., 150 m was used for the value of the 0- to 300-m ring). We compared regression models using SigmaPlot 9.0 (Systat Software, Inc. 2005). Models were evaluated using R^2, adjusted R^2, Durbin–Watson statistic, and residual analyses. To assess the level of human foot traffic, we calculated a DRKm for the total number of people seen within each ring.

Correlations were done to test if group size was associated with distance from the lab clearing, both including and excluding singletons. To test if the proportion of singletons was correlated with distance from the lab clearing, we created 11 bins, of 300-m increments, and correlated the bin distances with the calculated proportions of singletons within the bins. Pearson's correlation was used to determine if perpendicular sighting distance from the trail was affected by distance from the lab clearing. Distance from the lab clearing for each encounter was calculated using ArcMap 10 (ESRI, Inc. 2010).

Spatial distribution.—To assess changes in foraging areas through time, we delineated aggregations of peccaries based on natural clusters of group sightings over time for trails 1 and 3, the trails with sufficient data. We divided each trail into 300-m segments and calculated the percentage of times we walked the segment that included at least 1 peccary sighting. We also calculated an index of dispersion (variance/mean) for groups to determine how peccaries are dispersed in La Selva. We used 300-m segments as our sampling unit.

Population estimates.—The population of peccaries in La Selva was estimated by censusing a 12.5-m strip on each side of the trail; 12.5 m was chosen a posteriori given that beyond 12.5 m the detectability of peccaries dropped considerably and was consistently low. Each survey day was then considered a replicate and estimates were calculated using the following formula: $\hat{D}_i = [\bar{y}_i/(L_i \times 0.025)]$, where $\hat{D}_i$ is the number of groups per square kilometer, $\bar{y}_i$ is the average number of groups seen each survey day for trail i, L_i is the total survey distance (in km), and 0.025 is the width of forest censused (in km). Numbers of individuals for each trail were then estimated by $\hat{d}_i = \hat{D}_i \times \bar{g}_i$, where $\bar{g}_i$ denotes average group size. Mean group size was calculated for each trail independently to keep the scale of estimates the same. Assuming the 2 estimates ($\hat{D}_i$ and $\bar{g}_i$) to be independent of one another, $SE(\hat{d}_i) = \sqrt{\hat{D}_i^2 s_{\bar{g}_i}^2 + \bar{g}_i^2 s_{\hat{D}_i}^2 - s_{\bar{g}_i}^2 s_{\hat{D}_i}^2}$, where s_{D_i} and s_{g_i} denote the standard errors of $\hat{D}_i$ and $\bar{g}_i$, respectively (Goodman 1960). We did not estimate densities for the entire station, but rather kept densities specific to each trail, because of the many arbitrary decisions involved (e.g., for what area of La Selva is a particular trail representative, especially in light of the effect of the distance from the lab clearing?).

Historical perspective.—To assess changes in abundance over time of both collared and white-lipped peccaries, we reviewed pertinent published sources for Costa Rica's Caribbean lowlands and obtained unpublished historical data from a variety of sources. These unpublished sources include a 1979–1986 logbook in which researchers at La Selva recorded mammal sightings. We used unpublished data collected by D. Graham, who from June 1991 to March 1992 recorded mammal observations, their location, group size, time of day, and behavioral notes. We also used unpublished data from B. E. Young, who was at the time the full-time director of La Selva Biological Station, and A. Illes, who recorded mammal sightings intermittently between 1994 and 1997. To assess the state of peccary populations in the 1990s we calculated the

percentage of mammal sightings that were peccaries, average group size, and largest group. We only included observations of mammals before 1900 h because of the behavior of peccaries and the focus of this study on diurnal sightings. To evaluate historical peccary populations further, we queried knowledgeable local residents and scientists who have vast experience working in Costa Rica's Caribbean lowlands during different time periods; this included an individual who hunted regularly in the area in the 1950s and 1960s.

We used Minitab version 15 (Minitab, Inc. 2007) for all statistical tests, unless otherwise noted, and ArcMap 10 (ESRI, Inc. 2010) for all geographic information system analyses. This project was undertaken with the approval of the University of Kansas Institutional Animal Care and Use Committee. All animal handling protocols were in accordance with the guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Results

We sighted collared peccaries 231 times (217 diurnal and 14 nocturnal); no white-lipped peccaries were observed. Group size ranged from 1 to 19, with averages of 3.94 ($SD = 3.74$, median = 2) and 5.48 ($SD = 3.79$, median = 4) with singletons included or excluded, respectively. Singletons made up 34.4% of sightings. Mean group radius was 7.7 m ($SD = 9.00$ m) with a range of 0.25–50 m. Animals that were on the trail or within 1 m of the trail represented 47.6% of sightings. The detection rate within 12.5 m from the trail stayed relatively constant, and then dropped, suggesting a significant proportion of groups beyond this distance might have been missed. Collared peccaries were the most frequently encountered mammal during the survey, comprising 27.3% of sightings.

Detection rates.—The DRHr for collared peccaries for diurnal and nocturnal surveys combined is 0.237, with a diurnal DRHr of 0.272 and a much lower nocturnal DRHr of 0.079. DRKm for diurnal and nocturnal combined, diurnal alone, and nocturnal alone are 0.220, 0.256, and 0.069, respectively. Peccaries were detected more often diurnally than nocturnally ($\chi^2_1 = 26.282$, $P = 0.0001$). The correlation between DRHr and DRKm is highly significant ($r = 0.973$, $P < 0.001$). Observer number did not significantly affect detection rates for peccaries ($F_{1,16}$ for observer number = 0.03, $P = 0.871$). However, rainfall did have a marginal effect, with fewer sightings in rainy periods (see next section). A goodness-of-fit test showed that peccaries were detected significantly more often by sight than by sound ($\chi^2_1 = 22.59$, $P < 0.001$).

Monthly DRKm varied considerably with a high of 0.421 in April 2006 and a low of 0.068 in December 2005 (Fig. 2). There were no significant trends through time ($r = -0.045$, $P = 0.851$). The DRKm values from the first 3 sampling months were quite different from one another, including the lowest and 2nd highest values. This had a large effect on the mean DRKm. Using the randomization procedure, we found that 95% of iterations stabilized within ±10% of the total DRKm at 584.38 km (194 survey days), and within ±5% at 778.98 km (257 survey days).

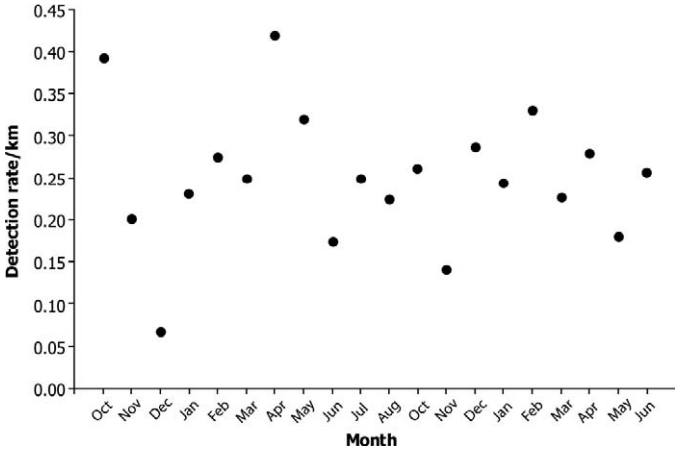

FIG. 2.—Monthly detection rates per kilometer of collared peccaries (*Pecari tajacu*) for all months surveyed.

Environmental factors.—The stepwise linear regression showed that among the variables mean daily rainfall (mm), air temperature (°C), maximum air temperature (°C), and minimum air temperature (°C) from the current and previous month, the only measured environmental factor associated with detection rates was rainfall, albeit only marginally significant ($R^2 = 0.188$, $P = 0.056$). This produced the relationship: detection rate = 0.348 − 0.00721 × mean daily rainfall (mm).

Primary and secondary forest effects.—No preference was detected between primary and secondary forest ($\chi^2_1 = 0.006$, $P = 0.940$). Group sizes in primary forest ($\bar{X} = 3.85$, $SD = 3.23$, median = 3) and secondary forest ($\bar{X} = 3.65$, $SD = 3.93$, median = 2) were not significantly different ($U_{113,86} = 11{,}952.5$, $P = 0.096$). Group radius was larger in primary forest ($\bar{X} = 9.30$ m, $SD = 10.08$ m, median = 6 m) than in secondary forest ($\bar{X} = 5.82$ m, $SD = 7.83$ m, median = 3 m; $U_{79,47} = 5{,}523.5$, $P = 0.010$). The proportion of singletons in primary forest (29.2%) was significantly smaller ($\chi^2_1 = 4.16$, $P = 0.041$) than in secondary forest (44.2%). Perpendicular sighting distance to trail was significantly greater ($U_{113,85} = 12{,}642$, $P = 0.0003$) in primary forest ($\bar{X} = 4.42$ m, $SD = 5.03$ m, median = 4 m) than in secondary forest ($\bar{X} = 3.47$ m, $SD = 11.2$ m, median = 0.25 m). The proportion of sightings on and within 1 m of the trail was 36.3% for primary forest and 62.4% for secondary forest.

Diurnal and nocturnal differences.—For diurnal sightings, mean group size was 3.94 ($SD = 3.72$, median = 3), with 35% of the observations as singletons, whereas for nocturnal sightings the mean was 3.92 ($SD = 4.13$, median = 2), with 21.4% of observations as singletons. Group size was not significantly different between peccary groups sighted diurnally or nocturnally ($U_{215,13} = 24{,}997$, $P = 0.092$). Group radius was not significantly different ($U_{138,9} = 10{,}376.5$, $P = 0.183$) between diurnal sightings ($\bar{X} = 7.84$ m, $SD = 9.15$ m, median = 5 m) and nocturnal sightings ($\bar{X} = 5.03$ m, $SD = 6.08$ m, median = 3 m). The mean sighting distance from the trail was 4.03 m ($SD = 8.22$ m, median = 2 m) diurnally, and 2.96 m

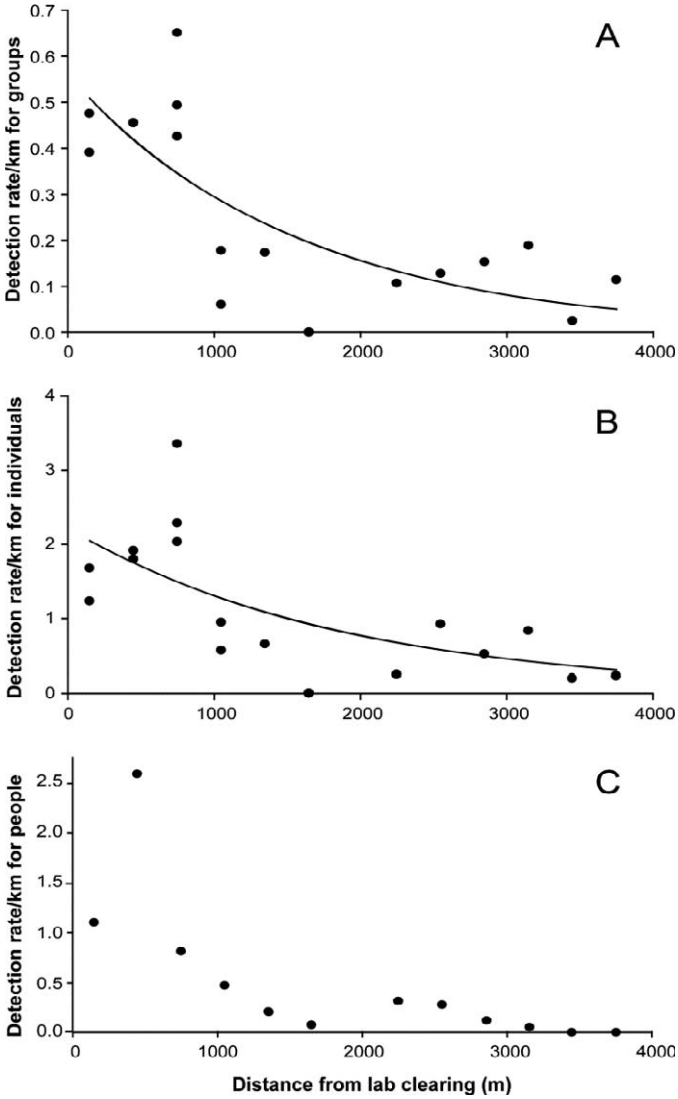

Fig. 3.—Detection rates per kilometer for varying distances from the lab clearing for a) groups of peccaries for each trail, b) total number of collared peccaries (*Pecari tajacu*) observed for each trail, and c) number of people observed in each 300-m segment.

(SD = 3.21 m, median = 2.5 m) nocturnally and not significantly different ($U_{216,13}$ = 1,487.5, P = 0.975). The percentages of sightings within 1 m from the trail were 38.5% and 47.9% nocturnally and diurnally, respectively.

Effect of lab clearing.—We evaluated a variety of regression models to determine the effect of distance from the lab clearing on number of peccary groups and total peccary numbers. Based on R^2, Durbin–Watson statistic, and plots of the residuals of various models, it was clear that the relationship between peccary variables and distance from the lab clearing was best expressed by a curvilinear relationship, particularly a single 2-parameter exponential decay function. The best-fit equation for number of peccary groups is: DRKm = 0.5603 $e^{(-0.0006\times DLC)}$, where DLC is distance from the lab clearing (R^2 = 0.5785 and P = 0.0004, n = 17; Fig. 3). The best-fit equation for total number of peccaries is DRKm = 2.2157 $e^{(0.0005\times DLC)}$ (R^2 = 0.4442, P = 0.004, n = 17; Fig. 3). In other words, the number of peccary groups and the number of total peccary individuals is higher near the lab clearing. DRKm for foot traffic was typically higher closer to the lab clearing, especially at 300–600 m (Fig. 3).

Group size was not significantly correlated with distance from the lab clearing, regardless of whether singletons were included (r = 0.093, P = 0.175, n = 215) or excluded (r = 0.086, P = 0.312, n = 140) in the analysis. Moreover, the proportion of singletons, in 300-m bins, was not significantly correlated with distance from the lab clearing (r = –0.372, P = 0.259, n = 11). Perpendicular sighting distance from the trail was not correlated with distance from the lab clearing (r = 0.058, P = 0.399, n = 217).

Spatial distribution.—Because of the different number of times each trail was walked, spatial analyses were completed separately for each trail. On trail 1, peccaries appear to be relatively regularly distributed. However, when distributions are plotted by year, it becomes obvious that peccary groups are clumped in several areas. To elucidate this pattern further, it can be observed from Fig. 4 that on several 300-m segments of the trail (segments 3 and 6–9) peccaries were rarely seen compared to segments 1, 2, 4, and 5. On trail 3, this pattern is repeated in that segments vary widely in the probability of a peccary encounter (Fig. 4). To support these findings, the dispersion indexes ($s^2/\bar{X}$) for groups on trails 1 and 3 are extremely high (4.83 and 3.98, respectively). These high values suggest a clumped distribution. However, on trails 2 and 4 the dispersion indexes for groups (1.6 and 1.1, respectively) suggest a random distribution.

Population estimates.—Estimated peccary group densities range from 3.7 groups/km^2 on trail 2 to 20.7 groups/km^2 on trail 1 (Table 1). The densities of individuals range from 19.1 peccaries/km^2 on trail 4 to 65.9 peccaries/km^2 on trail 1 (Table 1).

Historical perspective.—The La Selva logbook from 1979 to 1986 has a total of 1,009 mammal sightings, 75 of which are of peccaries. Only 3 peccary sightings occurred in 1979, all of which were white-lipped peccaries. White-lipped peccary sightings at La Selva after 1979 cannot be confirmed, because observers were uncertain about which peccary species was seen.

D. Graham (Florida International University, pers. comm.) cited a total of 271 diurnal mammal sightings. Mammal sightings were recorded for 154 days, and 67 of the total sightings were of collared peccaries, 39 of which occurred in the lab clearing. Mean group size was 3.6 (SD = 3.6) and 4.9 (SD = 3.8) including and excluding singletons, respectively. The largest group size observed was 15–20 individuals, and 32.8% of his peccary sightings were singletons.

Mammal observations by B. E. Young and A. Iles collected during 103 days between 1994 and 1997 include 207 sightings, 47 of which were of collared peccaries. Mean group size for this data set including and excluding singletons, respectively, is 5.03 (SD = 6.09) and 7.25 (SD = 6.62). The largest group was 24 peccaries, and 23.4% of their sightings were of singletons.

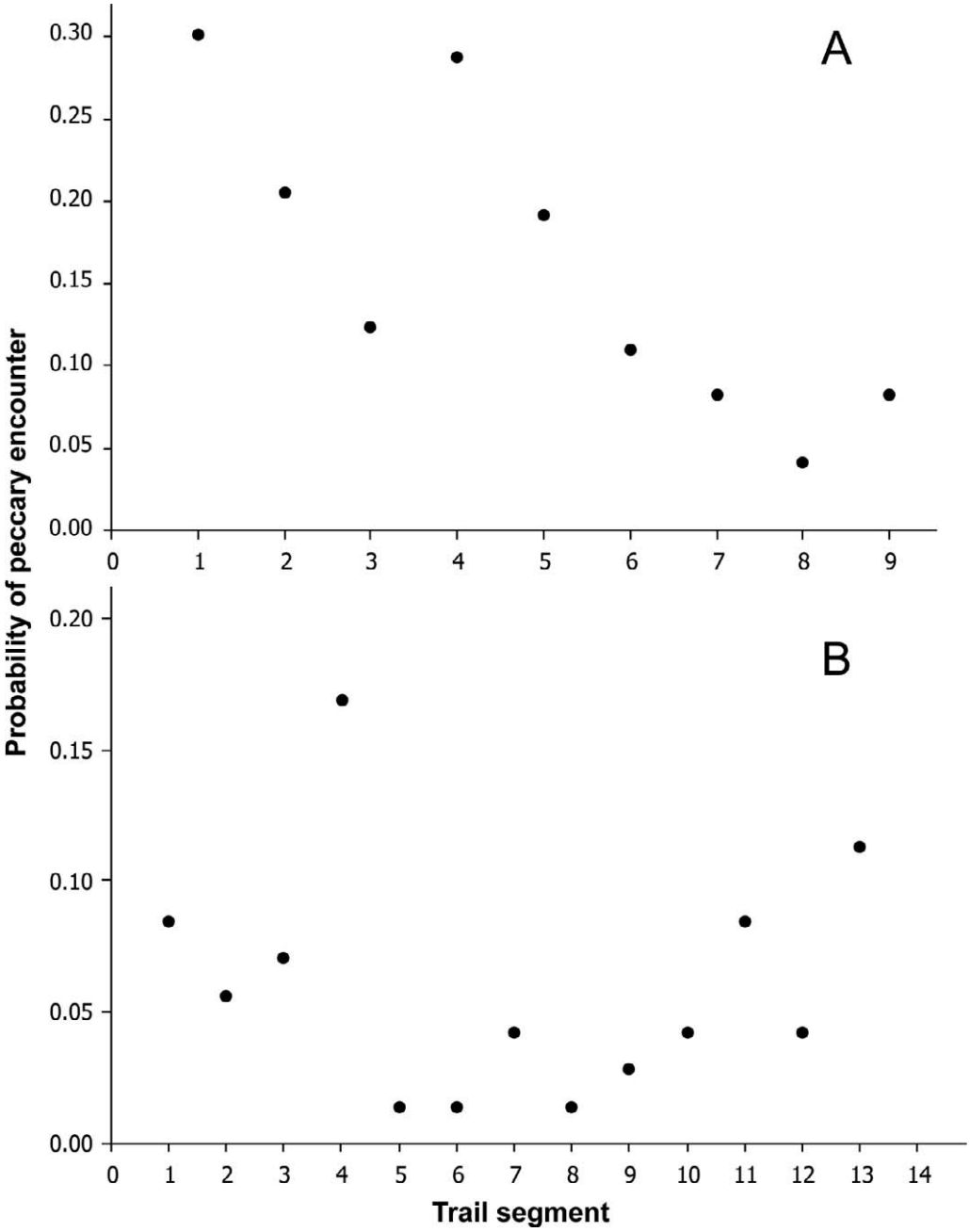

Fig. 4.—Probability of encountering at least 1 collared peccary (*Pecari tajacu*) for each 300-m trail segment throughout the entire study for a) trail 1, and b) trail 3.

Table 1.—Estimates of group and individual density with associated standard errors for each diurnal trail, for collared peccaries (*Pecari tajacu*).

Trail	Density of groups (no./km^2)	*SE* of group density	Density of individuals (no./km^2)	*SE* of individual density
1	20.66	1.855	65.92	8.29
2	3.73	0.949	21.05	6.96
3	8.27	1.164	38.72	6.75
4	4.25	0.886	19.05	5.78

Historical information and comments gathered concerning white-lipped and collared peccaries at La Selva and elsewhere in the Caribbean lowlands are presented in Table 3, and are represented graphically in Fig. 5.

Discussion

Collared peccaries were the most frequently sighted mammal during this study. They are considered common at La Selva Biological Station because peccary groups are seen daily around the lab clearing and on the neighboring trails. No

Table 2.—Estimated mean group size, largest group observed, and the prevalence of singletons for the collared peccary (*Pecari tajacu*) in various parts of its range. NR = not reported.

Location	Mean group size	Largest group	Singletons	Citation
Costa Rica				
Singletons	3.94	19	34.4%	Current study
No singletons	5.48			
Argentina	5.4	12	NR	Altrichter 2005
	23.2	50		
	3	5		
Brazil	9	NR	NR	Keuroghlian and Eaton 2008
Brazil	4.3	10	NR	de Azevedo and Conforti 2008
Brazil	9	NR	NR	Keuroghlian et al. 2004
Mexico	3.3	12	Groups of 1–4 commonest	Mandujano 1999
	4.5			
Panama	3.1	NR	44%	Robinson and Eisenberg 1985
Peru	NR	NR	42%	Kiltie and Terborgh 1983
Venezuela	6.5	NR	29%	Robinson and Eisenberg 1985
Arizona	8.5	53	4 instances	Knipe 1957[a]
Arizona	8.6	NR	NR	Day 1985[a]
Arizona	12	NR	NR	Day 1985[a]
Arizona	7.9	NR	NR	Sowls 1984[a]
Arizona	11.2	NR	NR	Byers and Bekoff 1981
Arizona	8.8	19	No	Byers 1980[a]
Arizona	8.1	18	NR	Bigler 1974
Texas	5.47	NR	NR	Green et al. 2001
Texas	4	NR	27%	Gabor and Hellgren 2000
Texas	14.4	27	No	Bissonette 1982[a]

[a] As cited by Sowls (1997).

white-lipped peccaries were observed during this survey, nor have any been observed at La Selva for > 35 years.

Group size.—Mean group size for collared peccaries at La Selva is within the range of those reported in the literature (Table 2). Herds in the northern, and more arid, parts of the range are larger than in Central and South America. Factors potentially accounting for small group sizes in the tropics include hunting pressure, response to environmental conditions, distribution of food resources, or observer visibility (Green et al. 1984; Sowls 1997). We discount hunting pressure as a cause for small group size, even though poaching still occurs at La Selva and in the adjacent Parque Nacional Braulio Carrillo, because peccary abundances are relatively high (see below) and because our survey was not conducted at the periphery of the reserve, where poaching is more likely to occur. Understory growth at La Selva may account for reduced sightings at a critical distance from the trail, because vegetation can obscure part of a group. Torrealba and Rau (1994) estimated mean group size for several herds at La Selva, based on the number of individuals entering sleeping sites, and reported averages of 9–27 peccaries, with an average size of diurnal subgroups of 3–5. Thus, the small group sizes seen here can reflect that peccary herds in the tropics may be rather fluid and disband into smaller subgroups during the day.

Throughout the range of collared peccaries, singletons range from being infrequently seen to comprising up to 44% of all sightings (Table 2). At La Selva, 34.4% of sightings were of singletons, which is higher than proportions reported in Texas and Venezuela, but lower than in Panama and Peru (Table 2). Differences in the number of singletons have been found in tropical deciduous and semideciduous forests (Mandujano 1999), and the number of singletons likely differs in response to environmental conditions and herd dynamics. Singletons were thought to be old males that had left the group (Leopold 1959) or disabled animals (Schweinsburg 1971), but Oldenburg et al. (1985) found solitary young and old peccaries that were healthy. Keuroghlian et al. (2004) found no evidence of subgrouping for prolonged periods of time in Brazil, but 1–3 individuals would often forage separately for several hours. It is unlikely that the high proportion of singletons seen at La Selva represents old males or disabled animals, but rather evidence that herd stability and cohesiveness differs across the tropics. The high occurrence of subgroups and singletons may be due to environmental factors because small groups remained common throughout all seasons of our study, and in arid regions, subgroups and singletons occur in higher frequencies following periods of precipitation and when vegetation appears to be most dense (Oldenburg et al. 1985).

The physical spread of a peccary group has rarely been quantified or addressed in the literature. Variability in mean group radius is probably due to environmental conditions, group size, interactions among herd members, foraging, and threat of predation. In Texas, 94% of singletons and subgroups have a separation distance from the main group of 100–599 m, although it may be as far as 1,400 m (Oldenburg et al. 1985). Unfortunately, no data are available to compare the spread of individuals in their functional subgroups to our mean spread of 7.7 m.

The large proportion of sightings close to the trail (47.6% within 1 m) could be a consequence of difficulty in sighting peccaries through the dense understory, or more likely because peccaries prefer to move or aggregate on more open trails (e.g., for ease of movement, foraging resources, heightened predator detection, or a combination of these). The dense understory may account for reduced visibility at a critical distance from the trail; however, it is unlikely that detectability greatly declines 1 m from the trail. Peccaries can be noisy as they forage and move, are fairly large animals, and can be detected by smell. The estimated distance from the trail beyond which a significant proportion of peccaries were missed was 12.5 m, and although shorter distances likely have higher detection probabilities, the difference in detection is small within the 25-m strip. Therefore, the large proportion of peccaries close to trails almost certainly represents a behavioral preference.

Detection rates.—The survey was walked at ~1 km/h and, therefore, DRHr and DRKm are very similar. We use DRHr

Table 3.—Quotations illustrating historical and current peccary populations (*Pecari tajacu* and *Tayassu pecari*) in the Caribbean lowlands. Citations demarcated with an asterisk (*) are based upon our correspondence with the observer. The text provided herein for Isaías Alvarado-Díaz represents our translation from his original Spanish. With the quotations used here, we remain faithful to the observers' wording and ideas, although some text that they provided is omitted for clarity, focus, and space concerns. Local names in Costa Rica for white-lipped peccaries are cariblanco and chancho de monte and to a lesser extent javali. Waree (variously spelled as wari and wuari) is the name used throughout Nicaragua for white-lipped peccaries and Carr (1967) uses that name for his observations at Tortuguero in extreme northeastern Costa Rica. Saino is the name used throughout Costa Rica and Nicaragua for collared peccaries. Brackets at the end of the quotation indicate the locality referenced by the observer.

Observer or citation	Quote
Bard (1855:281–224), 1850s	"Among the wild animals most common in Central America, is the peccary [*P. tajacu*] . . . best known by the Spanish name Savalino. There is another animal, something similar to the peccary . . . called Javalino by the Spaniards, and Waree [*T. pecari*] by the Mosquitoes . . . swarm all over the more thickly-wooded portions of the country. . . . They go in droves, and are not at all particular as to their food, eating ravenously snakes and reptiles of all kind. They have also a rational relish for fruits . . ." [Nicaragua's Caribbean coast]
Alston (1879–1882:110), 1860s	"In Costa Rica, Dr. v. Frantzius informs us that the White-lipped Peccary is found in great droves in the thick primeval forests of the warmer lowlands, but is also met with occasionally in the higher-lying mountain-woods, as at Cariblanco, near the Sarapiqui." [Costa Rica's Caribbean lowlands]
Belt (1874:30), 1860s	"Soon after we heard some wild pigs . . . or Wari . . . one of the boatmen leaping on shore soon shot one. . . . These Wari go in herds of from fifty to one hundred." [Costa Rica–Nicaraguan border]
Slud (1960:76), 1950s	"Ominous are the clopping, champing noises of a herd of White-lipped Peccaries; unsettling is the heavy, growling 'woof' of a startled individual close at hand. . . . Mammals, except agoutis, squirrels, tayras, and monkeys are seldom to be observed" [La Selva]
Isaías Alvarado-Díaz (long-term resident of the Sarapiquí region, pers. comm., 26 February 2012), 1930s–2012	"El saino was one of the most hunted animals. There was a time when the 2 types were there, what they call the 'chancho de monte, el carablanco', the big one, which was found in large herds, but already in those time periods, of the 1980s, there weren't any in this area, those had become history. What there was a lot of was the saino, the little one, the one that now is very abundant at La Selva. What happened was that when they acquired an area that was abandoned pejiballales [*Bactris gasipaes*], then there, with that lost crop, they reproduced tremendously, and now there's a lot. That was one of the animals [the saino] frequently hunted, even though it was less commercial than the tepezcuintle [*Cuniculus paca*] . . . it was more for use at home, but yes, it hunted often. The cariblanco also was hunted a lot. I was still able to hunt it some sometimes, and they were very easy to hunt because their herds were so large. I was told there were herds of cariblancos of surely more than 100 animals. My father, told me that they got to kill, let's say 3 to 4 cariblancos, they had to kill them and leave, until the herd a while later left there, because nobody dared get close to where those animals were. There were an enormously large quantity of animals, but there was also a tremendous amount of hunting pressure. [La Selva region] When La Selva started being "La Selva", there were already none of those [*T. pecari*]. There were more historically. I think that in the years 1950s maybe, or something like that, there were already few herds. A small herd, that arrived from the far side of the Río Tirimbina and Bijagual, I was able to see them sometimes, and I was able to hunt an individual each time I found them. But I already was never able to find a herd of those, no, no, they were almost the same as the sainos, they would sense you and would leave. The herds were already very small, diminished, and thus, they were not as aggressive. . . . One of those herds, that was perhaps over 100 animals, travels kilometers . . . they would rummage, and eat, and that would be noticeable on the [forest] floor. . . . The herds were big, enormous, but with the proximity of Braulio Carrillo, months could go by where we wouldn't see tracks of cariblancos. But when they appeared, then the herds were large. . . . The sainos were hunted for their meat . . . but many said they didn't like the smell . . . but I made a well-cooked saino and it is a delicious meat. . . . Hunters told me, hunting cariblancos you could find them together with the jaguar. . . . There were cases where people would shoot, kill cariblancos, but maybe there were 3 hunters and 5 cariblancos were killed, so, they would leave 2 in the water . . . to go the next day, and the following day when they went, the jaguar had already taken and eaten one. My father would tell me that you'd have to go, shoot, and return to reload, and there was a big rock, and he would go, shoot, and get on top of the rock to reload the rifle, and he went, and jumped on the rock and the jaguar also jumped on the rock, and the animal [jaguar] left, but they both went to the rock to defend themselves, because it seems that a jaguar doesn't hunt a cariblanco in between those huge herds. . ..Of the commercial use of skins, it was the sainos that were sold. In that time period, when sainos were still hunted heavily, the skin would be sold where there were leather goods shops. The closest area where they would process leather was Venecia in San Carlos. But not the cariblancos. . . . For sainos the skins were used to make knife covers, belts, many things, but it was completely commercial. . . . For cariblancos, the skins were used for other things like self defense, if your neighbor's cattle came over to your property, one would grab hair of cariblancos or sainos and burn them and the cattle would leave the area, because for some reason cattle are scared of cariblancos, extremely scared. . . . In the 1930s the cariblanco was shot with a rifle and gunpowder. At La Virgen around 1945 there was a plantation of an African plant for the oil, about 800 hectares, and a great herd of cariblancos got into the field. My father and his colleagues killed them and they took them home. I remember my father coming home from work that day riding a horse with a cariblanco laid across the horse. In the 1980s there were only small groups of cariblancos, ~15. The saino and the cariblanco have similar diets. The saino, the little one, one could make the mistake to think there are too many. There aren't any in Braulio Carrillo, 85% of the sainos of Zurquí are in La Selva. [northeastern Costa Rica]
Daniel H. Janzen* (University of Pennsylvania, pers. comm., 7 September 2011), 1963–1970s	"What I recall in 1963–1968 is that La Selva (called Holdridge's finca back then, had lots of javali [*T. pecari*], which I had never seen before (other than in Osa in 1965). . . . I have no plus or minus memory of collared peccaries [*P. tajacu*]. There was an original station keeper "Rafa" and botero who also talked about them [*T. pecari*], as being a nuisance and common. I spent a lot of time in the La Selva forest back then picking up *Pentaclethra* seeds and other stuff . . . and I remember how the javali churned up the litter where they had passed. Then maybe about the early to mid 1970s, I recall the comment that the javali were disappearing (or had disappeared) and how strange." [La Selva]

Table 3.—Continued.

Observer or citation	Quote
Carr (1967:75), early to mid-1900s	"The other regular turtle eaters on the Bogue beach are. . .the ravening hosts of wari, or white-lipped peccaries. . . . The gangs of wari range from twenty to a hundred or more. They are direfully efficient scourge of all small animals. Where peccaries pass there are almost no small ground-dwelling animals to be found. Wari are so devastating that when I am asked why the green turtle chooses Turtle Bogue to cling to, out of all the thousands of miles of Caribbean shore that look like good turtle beach, I think first of saying: because peccaries find it hard to get there across the lagoon." [Tortuguero]
Richard K. LaVal* (Bat Jungle, Monteverde, pers. comm., 4 September 2011), 1968–1990s	"Once when I was doing the bat study at La Selva (1973–74), I saw a single white-lipped peccary near the trail. Never saw others or any collared during that year. Nor do I remember ever smelling peccaries there. During the OTS course in 1968 we neither saw nor smelled them, nor did people there ever mention the existence of peccaries. By the time I began making regular trips there with the course, in the early 90s, the collared group was there." [La Selva]
Paul S. Foster* (Reserva Bijagual, pers. comm., 7 November 2011), 1971	"the last known group of about 20 individuals [*T. pecari*] was shot in 1971 in a low area where they would bathe just northwest of the Reserve [Bijagual]. The common name for them around here is cariblanco—also the name of a town up the hill on the way to Vara Blanca." [Reserva Bijagual, Costa Rica]
Robert M. Timm* (University of Kansas, pers. comm.), 1974	"During a 12-day period in July 1974, I observed no peccaries of either species at La Selva" [La Selva]
James H. Beach* (University of Kansas, pers. comm., 19 March 2012), late 1970s	"(ca. late 1970s) they were the big ones [*T. pecari*]. . . . The smaller species [*P. tajacu*] are tiny compared to the big mammoth ones, which would scare the bejezus out of you if you snuck up on them—if for some reason you had no sense of smell and you COULD sneak up on them. I remember [someone] running full speed down the loop trail one day, scared out of her wits that the big peccaries were after her. . . . One time, it might have been that one, or another day, they were hanging around the *Carapa* tree eating the fruits (judging by their presence in the immediate area [snorts and snapping branches] and the mess in the mud and torn about shells and missing seeds, and smell). As I recall *Carapa* only had mast fruit episodes in irregular years and that year was one. That *Carapa* tree was on the far loop trail, about 1/4 of the way out where the trail crossed a small stream (*Sabalo esquina*?). . . . I only saw them at the *Carapa* once." [La Selva]
Deborah A. Clark* (La Selva Biological Station, pers. comm., 8 October 2011), 1980s	"through most of the 80s, seeing a group of even so few as 4 collared peccaries was a big deal. To the point you'd report it at meals, etc., as a special thing. Most days you'd see none, and there were NO WALLOWS on the forest floor. Then, there was an abrupt explosion of piggies, and in my memory is it happened ca. 1988–89 (?). All of a sudden (it seemed) there were more sightings and growing groups size. Eduin Paniagua, the Forest Guard at the time, came to us all preoccupied, saying the pigs were ruining the forest and that they needed to be culled back to 'normal' (for him) levels. We presumed this was due to finally getting illegal hunting down in the reserve, but of course there are no data on either to test this. And this is when pig-wallows began to appear on the forest floor." [La Selva]
Amos Bien* (Rara Avis Rainforest Lodge and Reserve, pers. comm., 2 November 2011), 1963–2010	"When I was at La Selva from 1977–81, I never saw a single peccary of any type. I saw rare tracks. On recent visits, La Selva gave me the impression of being overrun by collared peccaries in small groups. Up the hill, at el Plástico–Rara Avis [500–700 m], the story is different: – The prisoners I interviewed told me that they would sometimes shoot the abundant white-lipped peccaries from the balcony while they were there from 1963–65. – From my arrival there in 1983 until the early 1990s, I would see occasional tracks, of collared peccaries I assumed, because the tracks were always only one or two individuals. – However, in 1993, I saw a pair of white-lipped peccaries close-up in broad daylight on the road into El Plástico. We have had no further sightings. – However we have frequent and growing sightings of collared peccaries, although subjectively much less abundant than at La Selva. There are abundant tracks of single individuals or pairs, but not of herds. I cannot tell apart the tracks of the two species. A camera-trapping project at Rara Avis last year [2010] also captured collared, but not white-lipped peccaries." [northeastern Costa Rica]
Gary S. Hartshorn* (World Forestry Institute, pers. comm., 2 November 2011), 1970–1980s	"My earliest recollections are from my long-term stints (usually ten days straight at La Selva, then four days home in SJO) during 1970 and the first eight months of 1971. During my post-doc research on gaps (1972–1975), I typically spent four nights at LS and three at home. Post-1975 till my 1989 move to D.C., I typically was at La Selva several days per month. The long-time foreman, Rafael Chaverria (that OTS inherited from prior owner Les Holdridge), was my foremost teacher of local natural history. I regularly talked with him about trees as well as wildlife; he was an excellent observer and woodsman. I recall him being excited to tell me (in the early 70s) that he saw the tracks of a sizeable herd (>20?) of white-lipped peccaries ("cariblancos") where they had crossed the far-side of the Loop Trail. I asked him how he knew they were cariblancos, not "sainos" (= collared peccaries)? He said by the size of the hoof-prints and that there was no odor so typical of collared peccaries. Also, that he had been a hunter and knew well the habits of cariblancos.

Table 3.—Continued.

Observer or citation	Quote
	Interestingly, an older boatman (Manuel Maria) based in Puerto Viejo also told me stories about hunting cariblancos in the swamps of what is now La Selva. According to these knowledgeable hunters, cariblancos moved in fairly large herds over sizeable geography, possibly migrating into the lowland swamps to feed on *Carapa nicaraguensis* (old name = *C. guianensis*) seeds.
	In the 70s and probably most of the 80s, collared peccaries were rather rare at La Selva. I might smell or see them just a few times per year. In the 70s we would occasionally hear shots (rifle or more typically shotgun) at night and assumed they were by poachers. I'm just speculating, but the abundance of squatters/hunters behind La Selva (i.e., in what became the Zona Protectora La Selva) may have been a factor in the low abundance of peccaries (both species?) at La Selva in the 70s. It wasn't till the late 80s with the consolidation of Greater La Selva and more effective patrols (e.g., Edwin Paniagua—another "reformed" hunter) that sainos became more abundant and noticeable in the front of La Selva. It wasn't just the lab clearing, but also sainos were quite noticeable in the Las Vegas annex (Bob Hunter's farm). If I recall correctly, sainos have been frequently seen along the first half of the STR [Sendero Tres Ríos] since the latter 90s.
	In setting up the altitudinal transect from La Selva to Volcán Barva (mid-80s) I remember encountering wallows in the muddy sections of the transect trail between 500 m and 700 m. Most importantly, there was no saino odor near these fresh wallows. Edwin Paniagua agreed with me that they were cariblanco wallows. But, to my knowledge, we never had any confirmed sightings of cariblancos along the transect trail." [northeastern Costa Rica]
Don E. Wilson* (Smithsonian Institution, pers. comm., 2 November 2011), 1968–1970s	"we had no sightings of cariblancos on the transect during our early surveys of the ZP [Zona Protectora]. I also never saw peccaries of any sort at La Selva in the early days. I first went in there in dry season of 1968. I also don't recall peccaries of any sort in there in 1970–71." [northeastern Costa Rica]
F. Gary Stiles* (Universidad Nacional de Colombia, pers. comm., 12 September 2011), 1960–1980s	"I never saw white-lips at La Selva, and not very many collared peccaries either. I recall several encounters in the late 1960s when I was working way out the Central Trail [at La Selva] . . . and only a few encounters in the early 1970s when I was spending most of my time at La Selva. On several occasions I ran into hunters with dogs towards the back of the property, and I suspect that the population was quite low . . . as I recall, I never saw any group larger than 3–4 animals. My visits to La Selva in the 1980s were more sporadic, often associated with OTS courses. I do recall seeing two groups of around 6 on one visit in the late 1980s, one out the East Boundary and one on the Central Trail (I suppose it could have been the same group, no way to tell but the distance between the encounters was probably ca. 500? m). I remember this because one of the groups was relatively aggressive (I was considering finding a tree!), in sharp contrast to my encounters in the 1970s, when the peccaries were invariably very skittish." [La Selva]
Joseph Wunderle* (International Institute of Tropical Forestry, pers. comm., 7 December 2011), 1970s	"I first went to La Selva in January 1973, and then on followup trips (1979), but do not recall seeing peccaries (either species). Heard some and saw some footprints and digging evidence in 1973, but do not know which species." [La Selva]
David Janos* (University of Miami, pers. comm., 23 November 2011), 1973–late 2000s	"When I lived at La Selva from 1973 to 1975, I very rarely encountered any peccaries. Only one encounter sticks in my mind, and that was just two small collared peccaries one of which got a bit aggressive with me. I've never seen a cariblanco or anything that I recognized as a sign of one at La Selva or on the transect [La Selva–Volcán Barva].
	My impression is that as collared peccary abundance increased at La Selva through the '90s, it also increased in the lower reaches of the altitudinal transect (especially below 1070 m). I can't remember when, but perhaps in the '90s I was walking on the west bank in the second growth over towards Tosi's house, and ran into a huge herd of what might have been 20–30 animals (including young). Also, sometime in the late 2000s I was out near the end of Sendero Sarapiquí when I came upon a mama saino and two babies that weren't any bigger than American footballs.
	I recall Rafael Chaverria telling me that when he was a young man he hunted cariblancos in the La Selva swamp.
	I agree with Gary [Hartshorn] that the most likely explanation for the disappearance of cariblancos from La Selva pre-OTS, and perhaps the low numbers of sainos in the '70s most likely was hunting pressure especially at the back and around the edges of La Selva." [northeastern Costa Rica]
Mirjam Knörnschild* (University of Ulm, pers. comm., 12 December 2011), 2000s	I have seen peccaries crossing the bridge several times [a ~1.5-m-wide, ~100-m-long walk bridge crossing the Río Puerto Viejo] . . . always from the comedor [dining room] side to the lab clearing side . . . I don't know whether me sitting close to the lab clearing side prevented them from crossing both ways—they always seemed to be genuinely surprised to find someone sitting in their way. Twice, I got up and let them pass because they couldn't muster the courage to squeeze by . . . the rest of the times they walked past right behind my back. I always thought it must have been part of the group that hung out at the lab clearing because they were so habituated. The group that crossed the bridge was rather small (once, it was only 4 peccaries; the rest of the times there were around 6–8 peccaries). They crossed the bridge between 4:30 and 5:30 a.m., always when it was still dark." [La Selva]

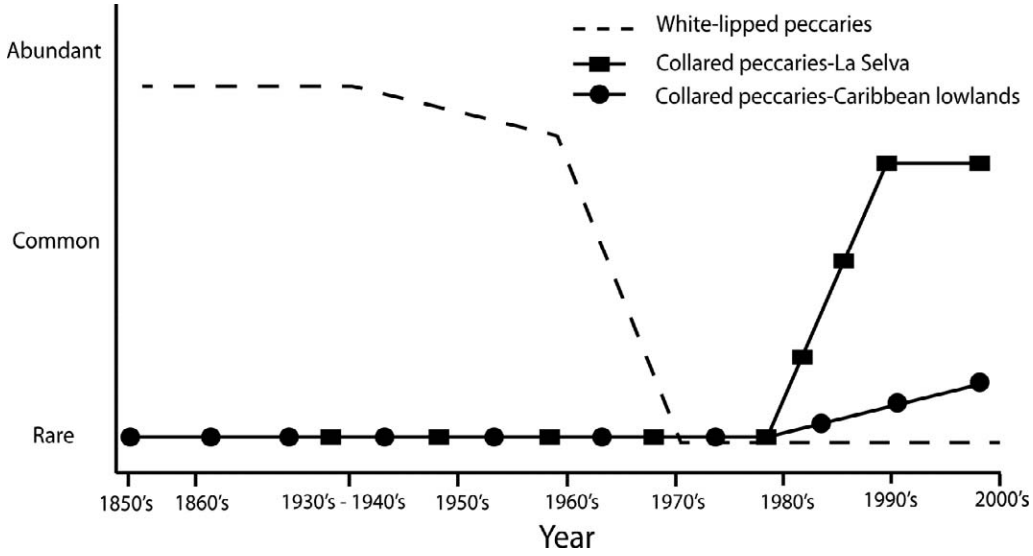

Fig. 5.—Reconstructed hypothesized changes in the abundances of white-lipped peccaries (*Tayassu pecari*) and collared peccaries (*Pecari tajacu*) in the Caribbean lowlands of Costa Rica and La Selva Biological Station based on historical literature and interviews (provided in Table 3).

and DRKm interchangeably, depending on which rate was appropriate for the analysis (e.g., DRKm was used for spatial analyses). The switch from 1 to 2 observers during the last 5 months of the survey did not affect DRHr, so we did not adjust the data for increased sampling effort. We recommend that when surveying collared peccaries, if 2 observers are available, it is better to have observers walk different transects simultaneously to maximize data collection. Collared peccaries can be loud and are easy to hear when threatened. However, during our survey we detected more peccaries visually than by sound. These findings give us confidence that we usually detected peccaries before they detected us and modified their behavior or position.

The DRHr and DRKm for diurnal surveys are much higher than for nocturnal surveys (14 of 231 sightings were nocturnal), and thus collared peccaries should be sampled diurnally. We excluded the nocturnal data from most of our analyses. Monthly DRKm did not show any significant trends. Moreover, monthly DRKm were quite variable, especially in the first 3 months, which included the lowest and 2nd highest DRKm. Using the randomization procedure, examination of our data shows that rapid surveys may be useful to detect the presence of a species, but may result in inaccurate detection rate estimates.

Environmental factors.—The only environmental factor that marginally affected DRHr was mean daily rainfall. Rainfall can affect fruit availability in the Neotropics (Keuroghlian and Eaton 2008), and in turn influence DRHr by altering peccary behavior and foraging strategies. Although collared peccaries may modify their diet during times of fruit scarcity (Bodmer 1990), the effects of seasonality and rainfall have been linked to changes in feeding pattern dispersion (Bigler 1974), home-range size, and level of activity and movement (McCoy and Vaughan 1990; Judas and Henry 1999). Variation in DRHr because of rainfall strongly suggests that care should be taken when comparing sites, or the same site, if surveys were conducted during different seasons. Surveys were never started during heavy rainfall, and in the event of rainfall during a walk, observers paused until conditions improved. Therefore, DRHr was not affected by visual obstruction due to rain, and was likely a result of some behavioral modification, although we do not have data to explore this further.

Primary and secondary forest effects.—Peccaries do not exhibit habitat preference between primary and secondary forest at La Selva, which is consistent with previous studies (Sowls 1997; Reyna-Hurtado and Tanner 2005; Tobler et al. 2009). Collared peccaries do show a preference for areas with canopy cover (Green et al. 2001), and an aversion to farmlands (Tejeda-Cruz et al. 2009). Hunting pressure also has an effect on habitat choice (Reyna-Hurtado and Tanner 2005).

Group size was not different in primary and secondary forest. However, the proportion of singletons in secondary forest is higher than in primary forest. Group radius and sighting distance were higher in primary forest. If secondary forest undergrowth makes peccary detectability more difficult, we might predict the greater sighting distance in primary forest and a higher proportion of singletons in secondary forest (some individuals in a small group are missed). However, recall that about one-half of the peccary sightings are within 1 m of the trail and many more sightings are within 3 m of the trail, so dense understory in secondary forest would not influence detectability. Additionally, ability of observers to visually detect peccaries in primary and secondary forest were estimated to be similar. The decreased group radius in secondary forest could indicate higher vigilance in areas of limited visibility or different dispersion of food sources.

The decreased perpendicular sighting distance from the trail in secondary forest was statistically different, but may not be

Table 4.—Estimated densities for the collared peccary in various parts of its range.

Locality	Density (individuals/km^2)	Citation
Costa Rica, La Selva	14 ± 1	Torrealba and Rau 1994
Panama, Barro Colorado Island		
1983–2010	6–35	J. G. Willis, Montclair State University, pers. comm.
2006–2011	18–25	
Panama, Barro Colorado Island	~1–35	Wright et al. 1999
Panama, Gigante	~1–12	
Panama	0–7	Wright et al. 2000
Panama, Barro Colorado Island	16	Eisenberg 1980[a]
Panama, Barro Colorado Island	9.3	Glanz 1982
Brazil, Pantanal, Matto Grosso	0.78	Schaller 1983[a]
Brazil, Caetetus Ecological Station	2.8–8.9	Keuroghlian et al. 2004
Brazil, Caetetus Ecological Station	4–15	Cullen 1997[b]
Brazil	1.9–11.6	Peres 1996
Guatemala		
Hunted	2.38	Novack et al. 2005
Unhunted	8.12	
Mexico, Chamela Biological Station	4.9 ± 1.6	Mandujano 1999
Mexico, Lacandon Forest	1.15–1.53	Naranjo et al. 2004
Mexico, Chamela	4.1–10.7	Mandujano 2007
Peru	5.6	Emmons 1987
Neotropics	12	Robinson and Redford 1986
Peruvian Amazon	3.3	Bodmer 1989[a]
Venezuela, Hato Masaguaral	8.5	Eisenberg et al. 1979
Venezuela, Hato Piñero	7.5–17	Polisar et al. 2008
Venezuela, Hato Piñero	7.5	Scognamillo et al. 2003
Arizona	4.5–11.5	Schweinsburg 1971
Arizona	3–4.7	Day 1985[a]
Arizona	2.1–4.5	Supplee 1983[a]
Texas	3.8–8.8	Low 1970[a]
Texas	3.3–11	Bissonette 1982[a]
Texas	2.01–9.15	Ilse and Hellgren 1995; Gabor 1997[c]
Texas	8.4–10.3	Gabor and Hellgren 2000

[a] As cited by Sowls (1997).
[b] As cited by Keuroghlian et al. (2004).
[c] As cited by Harveson et al. (2000).

biologically significant. The difference in means was 1 m, and the difference of the medians, which were the values statistically tested, was 3.75 m. Given the spatial scale in which peccaries move and forage daily, ±3.75 m from the trail may or may not be a signal of differential use of the open trails in primary and secondary forest. If this difference is biologically significant, it suggests that peccaries prefer to forage or move in more open areas closer to the trail in secondary forest, perhaps indicating differences in predator–prey interactions in these different forest types. Little is known about the distribution of peccaries and their predators through time and space, and prey-seeking and predator-avoidance or -fleeing behaviors, although Weckel et al. (2006b) showed jaguars prefer trails. At La Selva, the large predators of collared peccaries include the puma and jaguar. Jaguars have not been seen at La Selva for several years, although camera traps have captured this species along the Braulio Carrillo altitudinal transect connected to La Selva, and individuals likely reside or roam within the station, at least on occasion. Pumas are much more common, with visual sightings and confirmation via camera traps.

Effect of lab clearing.—Distance from the lab clearing did not affect group dynamics of collared peccaries, but did have a strong effect on the number of groups and the total number detected, with more observed near buildings. Number of groups and total number of peccaries exponentially decayed within 1 km and stabilized thereafter.

A higher number of peccaries seen closer to the lab clearing may be due to several factors that contribute to their true presence and detectability. First, peccaries may be more easily observed near the lab clearing because they are habituated to human activity, and there are greater and reliable food resources. Collared peccaries habituate readily, as reported for urban and nonurban peccaries in Arizona (Bellantoni and Krausman 1993). Individuals closer to the lab clearing are observed daily, sleep under buildings, and are less wary of observers than those at the back of the property. Peccaries closer to the clearing have repeated contact with humans and allow people to approach them, or they themselves approach people. Similar habituation was observed at La Selva in the 1990s, when peccary sightings in the clearing became common. Preference to gather in lab clearings has been observed on Barro Colorado Island for coatis (*Nasua narica*), and is presumably due to the plentiful availability and handouts of food (Kaufmann 1962; McClearn 1992). At La Selva, biologist M. Knörnschild had several encounters of peccaries crossing behind her on a ~1.5-m-wide, ~100-m-long bridge (Table 3). A. Romero (pers. obs.) observed a visitor holding bread fruit (*Artocarpus altilis*; Moraceae) in the lab clearing while a peccary ate it. In contrast, peccary groups in the back of the property are nervous and when detecting an observer would growl, woof, clack their teeth, and run away quickly, but this behavior increases detectability. In addition, the perpendicular sighting distance was not correlated with distance from the lab clearing, making it improbable that we overlooked peccaries in the back of the property. Thus, the higher number of sightings closer to the lab clearing represents the true presence of peccaries and not behavioral differences or differences in visibility.

Second, there may be more peccaries closer to the lab because high foot traffic of researchers and tourists could keep predators away. More large feline (puma or jaguar) scats and tracks (including sets of an adult with a juvenile) were seen farther back in the property, although at least 1 puma occasionally hunts within ~300 m of the lab clearing. Smaller feline scats (probably ocelot [*Leopardus pardalis*]) were seen throughout La Selva (A. Romero, pers. obs.). All large cat scat found contained peccary hair.

Third, collared peccaries probably are one of the most frequently hunted mammals within La Selva, and hunting likely takes place farther away from the lab clearing because it

is easier to enter the forest and hide from guards, researchers, and tourists. Although La Selva is one of the best protected areas in the tropics with trained park guards routinely patrolling, poaching still occurs. Hunters, hunting dogs, and evidence of hunting (butchered animals) are occasionally seen.

Finally, there may be environmental factors, such as the proximity to floodplains, that influence the abundance of peccaries. Collared peccaries can respond to habitat and resource differences at small scales (~1 km^2—Fragoso 1999). The lab clearing is at the confluence of 2 rivers, and flooding, with several meters of water, occurs yearly. Flood patterns affect this area ecologically, with floodplain soils being the most productive soils of the reserve, perhaps making the lab clearing more desirable for peccaries. However, floodplains are in close proximity to other surveyed trails (e.g., trail 4), which are far away from the lab clearing and do not have an abundance of peccaries.

Diurnal and nocturnal behavior.—It is obvious from DRHr that collared peccaries in the Caribbean lowlands of Costa Rica are diurnal–crepuscular animals. Although some authors suggest that this species is active during the night (Ellisor and Harwell 1969), our study shows that very few peccaries were encountered after dusk. Of the 14 nocturnal observations, several were of sleeping groups that were startled when approached. The sleeping groups were typically large and took advantage of manmade structures, for example, underneath stilted buildings in the forest or in the lab clearing. Other nocturnal observations occurred at the beginning of a survey and were of groups that were feeding, likely before retreating to sleep. We acknowledge that comparing data on group dynamics of 217 diurnal observations to 14 nocturnal sightings is not a balanced or robust design, but nonetheless we believe that this information can be used as a building block to understand peccary behavior after dusk.

Group size (median and mean) is not different for diurnal and nocturnal observations. Because of our small sample size of nocturnal observations, we could not statistically test if the proportion of singletons differed; however, examination of our data suggests that fewer singletons are observed at nighttime (21.4% versus 35%). This difference could be attributed to the survey technique itself (more difficult to see a singleton in the dark), or more likely, because fluid groups disband into smaller subgroups during the day and fuse back together at night. Neither group radius nor perpendicular sighting distance differs for diurnal and nocturnal observations, although the proportion of sightings within 1 m of the trail was 9% higher nocturnally. This suggests that peccary groups may not be increasing their vigilance by decreasing the spread of the group, nor changing their behavior to cluster on more open trails nocturnally. Given that our perpendicular sighting distance was not significantly different diurnally or nocturnally, we believe that the fewer observations of peccaries at nighttime are due to fewer peccaries being active, rather than difficulty in spotting them. Little information is available about the nighttime behavior of peccaries, and understanding nocturnal behavior will be important to further decipher diurnal group dynamics.

Spatial distribution.—A map of sightings over the course of the entire survey shows peccaries on all parts of the trails. However, for trails 1 and 3, separation of data by year reveals distinct areas where peccaries are frequently observed. These areas are relatively consistent year to year, although some shifts did occur. The results of the dispersion index reinforce these map observations, showing that peccary groups are clumped for trails 1 and 3. The random distribution for trails 2 and 4 may be a statistical artifact of low encounter rates. For this reason we graph only the probability of encounter for trails 1 and 3 (Fig. 4).

For surveys conducted on trails 1 and 3, the clumped patterns could have occurred because we were detecting several subgroups within the larger herd's home range, because different groups frequent the same spot with agreeable habitat characteristics such as food or shelter, because we repeatedly encountered the same group in the same spot, or because of a combination of these. For trails 2 and 4, the spatial distribution question is trickier to answer because of the lower number of sightings, although there also are areas of higher use. The spatial distribution patterns shown by our study may be more representative of the arrangement of subgroups, given the mean group size observed. However, our sampling methods do not allow us to determine how and why herds are distributed across the landscape.

Population estimates.—Estimating peccary densities is a difficult task, and a full understanding of the data, field methods, and statistical analysis is essential. We could not assign a density estimate for La Selva because of the conspicuous relationship between peccary detection rates and distance from the lab clearing. Rather, we estimated densities for each diurnal trail separately. Attempting to extrapolate densities for the whole station is problematic because there are too many arbitrary decisions to make (e.g., for what area of La Selva is trail *i* representative?). We, therefore, present peccary density estimates for groups (likely subgroups) and individuals for each trail. We believe that these trail density estimates will provide useful data on the state of peccary populations in La Selva today and provide baseline information against which future surveys can be compared for the purpose of establishing directionality and intensity of any trends.

Peccary densities at La Selva were estimated to be 19.05, 21.05, 38.72, and 65.92 individuals/km^2 for trails 4, 2, 3, and 1, respectively (Table 1). Although these estimates vary greatly within La Selva, they should not be taken as the lower and upper limits of densities for the entire property. For example, the density on trail 1 is much higher than for other trails. Yet, trail 1 is likely only representative of areas in La Selva that are close (~1 km) to the lab clearing, a relatively small area due to its proximity to the natural boundaries of the rivers. In contrast, trail 4, which traverses a large portion of the back area of the property, would likely be representative of a larger area. Therefore, it is inaccurate to combine these densities to calculate an average estimate for La Selva.

The estimate for trail 1 is higher than densities reported elsewhere in the Neotropics (Table 4). Estimates for trails 2–4

also are high, but within the range of densities found on Barro Colorado Island. These high estimates could be due to a number of factors. For example, both La Selva and Barro Colorado Island are among the best-protected field stations in the Neotropics, and hunting pressure is likely low. Additionally, La Selva has high net primary productivity, even higher than some areas in the Amazon, and thus may support higher abundances (D. B. Clark, La Selva Biological Station, pers. comm.).

Although density estimates provide informative data, caution should be exercised when comparing estimates from other sites or different time periods, or both. Densities of peccaries can fluctuate quickly, for example, a ~65% change in 4 months on Barro Colorado Island (Wright et al. 1999). Consequently, surveys done to compare densities at different sites should be done in a manner to account for population trends and fluctuations. Additionally, estimates calculated via different field or statistical techniques, or both, should not be directly compared. For this reason, we cannot compare the density estimate of Torrealba and Rau (1994) of 14 ± 1 individuals/km^2 to our estimates and assign a change or directionality to peccary populations. Peccary populations in the Caribbean lowlands of Costa Rica likely exhibit natural fluctuations through time. To understand larger-scale population changes, and the potential ecological impacts these changes have in the ecosystem, a thorough understanding of these populations in a current and historical perspective is imperative.

Historical perspective.—Published historical peccary densities for Costa Rica's Caribbean lowlands are limited. However, inferences on the populations of peccaries through time can be made from travel notes, published scientific accounts, and observations from individuals familiar with the area.

Early accounts from the Caribbean lowlands indicate that white-lipped peccaries were abundant, found in large herds, and regularly hunted. Samuel A. Bard (a pseudonym for Ephraim G. Squire [Bard 1855:281–224]) depicted white-lipped peccaries along Nicaragua's Caribbean coast as common, and described their "ravenous" feeding, which included snakes and reptiles (Table 3). Thomas Belt, the British naturalist, also commented on white-lipped peccaries along the Costa Rica–Nicaragua border from his travels up the Río San Juan, and mentions herds of "fifty to one hundred" in the lowlands (Belt, Table 3). Alston (1879–1882:110) described white-lipped peccaries in the Costa Rican lowlands as "found in great droves" and somewhat common at higher elevations (Table 3). These brief accounts indicate that in the 19th century white-lipped peccaries were abundant and found in large herds in the Caribbean lowlands.

White-lipped peccaries in the lowlands surrounding La Selva could be found in herds of more than 100 individuals in the 1930–1940s, even though they were heavily hunted. Evidence of large herds was apparent by how they affected the forest floor (Alvarado-Díaz, Table 3). The 1st written account of peccaries at La Selva is from Slud (1960) in the 1950s (Table 3). He comments on white-lipped peccaries but makes no mention of collared peccaries, which is a complete reversal of the peccary situation today. Around the 1950s, white-lipped peccary populations were decreasing in the Caribbean lowlands, although large populations still persisted (Alvarado-Díaz, Table 3).

Historically, white-lipped peccaries were the most common of the 2 species at La Selva, being abundant in the lowlands and at higher elevations on Volcán Barva at El Plástico–Rara Avis (500–700 m). Through the early to mid-1960s, a La Selva staff member considered them a nuisance and their effect on the leaf litter was apparent (Janzen, Bien, Table 3). Large herds were hunted, and by the late 1960s white-lipped peccaries were disappearing (Janzen, Bien, Alvarado-Díaz, Table 3). The last herd of white-lipped peccaries in the Río Bijagual area (at approximately 300 m) was shot in 1971 (Foster, Table 3).

In the 1970s, both white-lipped and collared peccaries were present in low densities at La Selva, and likely throughout the elevational transect to Braulio Carrillo. Through the 1970s, evidence of white-lipped or collared peccaries was limited to few observations of individuals or tracks. At La Selva, a herd of > 20 white-lipped peccaries was seen by Rafael Chaverria (early 1970s), and a single individual was seen by Richard LaVal (1973–1974) (LaVal, Hartshorn, Table 3). The last reported sightings of white-lipped peccaries at La Selva are in the 1979 logbook, where 3 observations of small groups (~10, 6, and 3 individuals) were recorded (1 observation confirmed with original observer [Beach, Table 3]). Throughout the 1970s, herds of white-lipped peccaries must have been greatly reduced, and collared peccaries were rare, both likely caused by hunting pressure (Table 3).

In the early 1980s, no evidence of white-lipped peccaries was noted at La Selva and collared peccaries were still rare. By 1983, locals reported white-lipped peccaries to be rare or absent in the elevational corridor (Pringle et al. 1984). Gary Hartshorn and Don Wilson (Table 3) never encountered white-lipped peccaries during their altitudinal transect work in the mid-1980s, although evidence of wallows believed to be from this species were seen, and few tracks of collared peccaries at El Plástico–Rara Avis were observed from 1983 to the early 1990s (Bien, Table 3). By the 1980s small groups, if any, of white-lipped peccaries (~15 individuals) inhabited the area, whereas collared peccaries were becoming abundant at La Selva (Alvarado-Díaz, Table 3).

This is consistent with the 1979–1986 logbooks at La Selva (Timm et al. 1989). It is difficult to assess the precise time of extirpation of white-lipped peccaries at La Selva because in the 1980s observers were uncertain of which peccary species were encountered. Nonetheless, these data provide information regarding peccary populations because in 1980, collared peccaries begin to appear regularly in the records, albeit in low numbers. Peccary populations, regardless of the species, must have been low from 1979 to 1986 because the proportion of peccary sightings to other mammal sightings during this time is low (0.01–0.14).

By the late 1980s, collared peccaries became more abundant at La Selva. Collared peccaries were commonly seen, and their

growing group size and physical impact on the forest floor, such as the appearance of wallows, were apparent (Clark, Table 3). Interestingly, a forest guard believed that collared peccaries were becoming a nuisance (Clark, Table 3). By the 1990s, collared peccary groups were conspicuous around the lab clearing (D. Graham, Florida International University, R. K. LaVal, Bat Jungle, Monteverde, R. M. Timm, University of Kansas, and B. E. Young, NatureServe, pers. comm.). We cannot use these data to calculate population densities or detection rates, but details are consistent with this study (mean group size, largest group, and percent singletons). The most quantitative historical data on collared peccaries at La Selva used radiotelemetry, documenting variability in group sizes and home ranges among different groups and months, and reporting a mean total annual home range of ~70 ha, and absolute density of 14 ± 1 individuals/km^2 (Torrealba and Rau 1994). The density and group dynamics, especially group size, of collared peccaries can be directly affected by competition with other species (Gabor and Hellgren 2000). Although not strong evidence, the similarity of group dynamics in these data sets possibly indicates that peccary abundances in La Selva throughout the 1990s and during this study were similar.

The last confirmed sighting of white-lipped peccaries in the La Selva–Braulio Carrillo complex was in 1993, when a pair was seen on the road to El Plástico (approximately 500 m). No white-lipped peccaries were seen at Rara Avis (in 2010), or at La Selva and higher-elevation sites in Braulio Carrillo (2003–current) via camera traps (Bien, Table 3; J. Hurtado A., La Selva Biological Station, pers. comm.). At higher-elevation sites, the abundance of collared peccaries may be increasing currently (Bien, Table 3). White-lipped peccaries have been extirpated from La Selva likely since the 1970s, and today are seemingly extirpated from the entire La Selva–Braulio Carrillo complex and have been since the 1990s. Small populations of white-lipped peccaries still persist in some remote areas of the Caribbean lowlands.

The extirpation of white-lipped peccaries, and decreased hunting pressure, may have allowed populations of collared peccaries to increase. Historical data to test whether the population density of collared peccaries has increased since the extirpation of white-lipped peccaries are not available, but all personal accounts and historical information support this hypothesis (Fig. 5). It appears that after the extirpation of white-lipped peccaries there was some lag time, but eventually white-lipped peccaries were replaced by collared peccaries. What remains a bigger challenge to discern is what ecological impacts, if any, occurred after the extirpation of white-lipped peccaries and the subsequent increase of collared peccaries.

Ecological impacts of shifting peccary populations.—The ecological impacts of shifting peccary populations will be difficult to assess and only inferences can be made based on the ecology and behavior of peccaries in other habitats. White-lipped and collared peccaries differ in key ecological aspects, but may perform similar ecological functions. White-lipped peccaries are larger, and live in large, cohesive herds (Sowls 1997; Fragoso 1998). Group size is variable, and likely is affected by hunting and habitat fragmentation, but often numbers in the hundreds. Anecdotal, historical reports describe herds of white-lipped peccaries of 300–2,000 individuals (Jardine 1836; Perry 1970; Sowls 1997). In contrast, collared peccaries live in smaller herds of 2–50 individuals, which are more fluid and often disband into subgroups (Sowls 1997). Home ranges of collared peccary are smaller than those of white-lipped peccaries (Sowls 1997).

Despite the ecological and behavioral differences between the 2 peccary species, striking similarities exist in how these species interact with, and alter, their environment directly and indirectly. In terms of diet, white-lipped and collared peccaries have considerable overlap for species and items consumed (Kiltie 1981; Barreto et al. 1997; Beck 2006; Desbiez et al. 2009), although white-lipped peccaries have a stronger bite force that allows them to handle harder seeds (Kiltie 1982; Beck 2006). White-lipped and collared peccaries affect plant density, composition, spatial distribution, and demography (Fragoso 1997; Beck 2006; Keuroghlian and Eaton 2009), likely in similar ways, with a particularly large effect on palms because palms make up more than 60% of their diet (Kiltie 1981; Kiltie and Terborgh 1983; Bodmer 1990; Beck 2006). The reported overlap in palm species consumption for both peccary species is 59%, and they prey upon the same seed species at similar frequencies (Beck 2006).

Peccaries affect plant communities, especially palms, via seed predation, seed dispersal, seedling trampling, herbivory, and foraging strategies, to the degree that they have been called ecosystem engineers (Keuroghlian and Eaton 2009; for review see Beck 2006). For example, peccaries are primarily seed predators (Kuprewicz, in press), but also can act as seed dispersers (Lazure et al. 2010). Peccaries account for high seedling and sapling mortality near parent trees, and the trampling and burying of seeds helps protect the seeds from predation by insects and increases germination rates, altogether affecting the spatial distribution of seedlings (Fragoso 1997; Silvius 2002). The magnitude of the impact peccaries have on their environments has been illustrated in several studies. For example, Wyatt and Silman (2004) showed an increase of uneaten palm seeds (5,340% for *Iriartea deltoidea* and 6,000% for *Astrocaryum murumuru*), and lowered seedling mortality when white-lipped peccaries are absent. Silman et al. (2003) documented that when white-lipped peccaries were absent during a 12-year period, the number of *Astrocaryum* seedlings increased by 70%, only to decrease by 71% after recolonization by peccaries. Hartshorn (1983:136) wrote: "The most striking aspect of the La Selva forest is the richness and abundance of subcanopy, understory, and dwarf palms ...." Today, however, the understory palms are not as abundant as in the early 1980s (R. M. Timm, pers. obs.). The effects that peccaries have on plants directly affect the plant community and must indirectly impact the community composition and diversity of other organisms.

White-lipped and collared peccaries also have important ecological impacts on animal communities, although these have been studied less than the impacts on plant communities.

Peccaries are ecosystem engineers because their wallows create higher β diversity, species richness, and a higher density of tadpoles, metamorphs, and adult anurans than found in ponds (Beck et al. 2010). Areas with collared peccaries have higher encounters of reptiles and amphibians, and more juvenile anurans than do peccary exclosures (Reider et al., in press). Peccaries appear to prefer seeds that are infested with insect larvae, which may result in population control of certain insects (Fragoso 1994; Silvius 2002). In addition, peccaries consume animals, including invertebrates, frogs, snakes, turtles, fish, eggs, eels, lizards, birds, and small rodents (Gamero Idiaquez 1978; Husson 1978; Fragoso 1999) in a manner that may significantly affect these populations (Carr, Table 3). Furthermore, the manner and extent to which peccaries transform their environment by altering the vegetation, leaf litter (Reider et al., in press), and other aspects of the habitat probably, directly and indirectly, have cascading effects on other taxa.

It is hypothesized that white-lipped peccaries outcompete collared peccaries because of their larger herd size and aggressive temperament (Altrichter and Boaglio 2004; Mendes Pontes and Chivers 2007). Although the effects of white-lipped peccaries on collared peccaries have not been studied, niche overlap among white-lipped peccaries, collared peccaries, and feral pigs (*Sus scrofa*) is highest between the 2 peccary species (Desbiez et al. 2009). Collared peccary populations that are sympatric with feral pigs have 5–8 times lower densities, smaller group sizes, and larger territories (Gabor and Hellgren 2000). Therefore, it is likely that a species with a higher niche overlap than feral pigs, the white-lipped peccary, could affect collared peccaries in similar, if not more drastic manners. Studies elucidating the degree of competition between peccary species, and the resulting impacts on population parameters, are important for understanding historical and current forest changes. Even though we lack historical density information of white-lipped peccaries at La Selva, it is likely that substantial numbers of large herds ranged throughout the Caribbean lowlands (Janzen, Table 3), and were heavily hunted (Alvarado-Díaz, Table 3). Given our historical information about peccaries at La Selva, collared peccaries were seemingly at low densities when white-lipped peccaries were common, perhaps due to direct competition or hunting pressure, or both, and that there was some lag time between the extirpation of white-lipped peccaries and the increase in collared peccary densities. White-lipped peccaries alter their environments in considerable ways (Silman et al. 2003; Wyatt and Silman 2004; Keuroghlian and Eaton 2009), so the transition period with no white-lipped peccaries and only small populations of collared peccaries probably produced a unique vegetation community at La Selva. Interestingly, this lag period corresponds to the rapid increase in research conducted at La Selva and to the concept of what constituted the "normal" La Selva forest. Although the 2 species differ, they share many traits that can result in collared peccaries having similar impacts on the environment today as white-lipped peccaries did historically. Thus, the current dominance of collared peccaries must not be considered as negative or abnormal without proper consideration and study of the relationship between peccary species and their impact on the environment, and a sound understanding of the area's complex ecological history.

Resumen

Entender la abundancia y la preferencia de hábitat de las 2 especies de sainos en bosques neotropicales es importante porque estas especies clave afectan muchos aspectos del ecosistema. En las tierras bajas del Caribe costarricense, llevamos a cabo muestreos a pie durante ~2 años para estudiar el comportamiento y tendencias poblacionales del saino (*Pecari tajacu*), y encontramos que son abundantes en la Estación Biológica La Selva y las tasas de detección fueron relativamente constantes a través del tiempo. Se obtuvo una tasa estable de detección después de 7–9 meses de muestreos. Las tasas de detección fueron similares en bosque primario y secundario, sin embargo, se encontraron algunas diferencias en la dinámica de grupo (el radio de distribución del grupo era más grande y la distancia de observación fue mayor en bosques primarios, mientras que el número de individuos solitarios fue mayor en bosques secundarios). Más sainos fueron vistos alrededor de las zonas abiertas rodeando el laboratorio, debido a varias posibles razones: habituación a la presencia de seres humanos, menos presión por depredación o cacería y otros factores ambientales o de hábitat. Los sainos están distribuidos de forma aglomerados y son más activos de día que de noche. Las densidades de sainos son relativamente altas en comparación con otros sitios neotropicales, con excepción de la Isla de Barro Colorado. El saino probablemente ha aumentado en abundancia en La Selva, aparentemente unos años después de la extirpación del cariblanco (*Tayassu pecari*), que eran abundantes en el área hace unos 40–50 años. El conocimiento de la dinámica de grupos, comportamiento y preferencias de hábitat del saino es esencial para las decisiones de manejo y los esfuerzos de conservación. Además, la evaluación de los cambios poblacionales debe considerarse cuidadosamente en un contexto histórico, con especial atención a cómo han cambiado las poblaciones del saino y cariblanco, y cómo estas especies afectan su ambiente.

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