

Do Neotropical peccary species (Tayassuidae) function as ecosystem engineers for anurans?

Harald Beck^{*1}, Paporn Thebpanya[†] and Melissa Filiaggi^{*}

^{*} Towson University, Department of Biological Sciences, 8000 York Road, Towson, MD, 21252, USA

[†] Towson University, Department of Geography and Environmental Planning, 8000 York Road, Towson, MD, 21252, USA
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Abstract: The concept of ecosystem engineering has catalysed novel approaches and models for non-trophic species interactions and ecosystem functions. Ecosystem engineers physically modify abiotic and biotic environments, thereby creating new habitats that can be colonized by a new suite of species. In the Peruvian Amazonas, we tested whether peccaries (Tayassuidae) function as ecosystem engineers by creating and maintaining wallows. Such wallows could be critical aquatic habitats and breeding sites for anuran species during dry seasons. We compared hydroperiods of 21 peccary wallows and 13 naturally formed ponds across three dry seasons and found that wallows had a consistently higher mean water surface area than ponds. We also examined the pH, dissolved oxygen and temperature, and found no significant differences in these parameters between water bodies. Wallows had a significantly higher density of tadpoles, metamorphs and adult anurans, as well as higher β -diversity and species richness than ponds. This study not only provides the first systematic evidence of the ecosystem engineering processes of peccaries, but also reveals the positive consequences of such for anuran species.

Key Words: anurans, ecosystem engineers, *Pecari tajacu*, non-trophic interaction, species richness, *Tayassu pecari*, wallows

INTRODUCTION

Species interactions in ecological communities are one of the most intriguing and complex research endeavours. Traditionally, most emphasis has been placed on trophic interactions such as competition or seed dispersal, but other types of interaction exist (Krebs 2008, Smith & Smith 2002). One interesting proposed type of non-trophic species interaction is ecosystem engineering (Jones *et al.* 1994). Ecosystem engineers are species that modify the conditions or the availability of resources for other species by causing or maintaining physical changes in the abiotic or biotic environment (Jones & Gutiérrez 2007, Jones *et al.* 1994, 1997). These physical state changes can have both positive and negative ecological consequences. Studies have shown that at the local scale (the scale of the engineered patch, *sensu* Wright & Jones 2004) the creation, modification, maintenance or destruction of habitats or resources can have either positive (Cuddington *et al.* 2009, Jones *et al.* 1997, Pringle

2008) or negative (Byers *et al.* 2006, Jones *et al.* 1997) effects on the abundance or diversity of sympatric species (Hastings *et al.* 2007). On the other hand, most studies found positive effects on a landscape level (Crooks 2002, Cuddington *et al.* 2007, Jones *et al.* 1994, 1997).

The beaver (*Castor canadensis*) is the classic example of an ecosystem engineer in North America (Jones *et al.* 1997, Stevens *et al.* 2007, Wright *et al.* 2000). By damming streams, beavers physically modulate water flow and cause formation of lentic ponds and wetlands. Felling of trees and creating wetlands has negative effects for antecedent inhabitants (Jones *et al.* 1997), while a new suite of plant and animal species subsequently colonizes the new habitats (Byers *et al.* 2006, Naiman *et al.* 1988, Wright *et al.* 2000).

Another ecosystem engineer is the bison (*Bison bison*), which creates dust wallows in grassland ecosystems (Bragg 1940, Gerlanc & Kaufman 2003). High soil compaction and bulk density in such wallows cause greater retention of rainwater and formation of aquatic habitats (Coppedge *et al.* 1999, Uno 1989). These modifications not only influence terrestrial plant distribution and richness (Polly & Collins 1984) but

¹ Corresponding author. Email: hbeck@towson.edu

also create critical breeding habitats for numerous animal species including insects, fishes, salamanders and anurans (Bragg 1940, Busby & Brecheisen 1997, Gerlanc & Kaufman 2003, McHugh 1972). Such non-trophic interactions are not captured with theoretical food web approaches or energy flow models (Buchman *et al.* 2007, Cuddington *et al.* 2007, Jones & Gutiérrez 2007).

In the Neotropics, Chacoan peccary (*Catagonus wagneri*, Rusconi), collared peccary (*Pecari tajacu*, Linnaeus) and white-lipped peccary (*Tayassu pecari*, Link) create and maintain wallows (Beck 2008, Gascon & Zimmerman 1998, SOWLS 1997). In arid habitats dust wallows dominate, whereas in more humid environments wallows are muddy and can form lentic bodies of water. Wallowing behaviour may be a form of grooming (SOWLS 1997), or a function of thermoregulation (Carrilla *et al.* 2002). Chapman (1936) provided one of the earliest accounts of a critical feature of peccary wallows when he noted: 'Here, even in the heart of the dry season, there were evidences of water' (see also Gascon 1995, Simberloff 1992, Zimmerman & Simberloff 1996).

In tropical rain forests the only other terrestrial and lentic water bodies are naturally formed ponds, which occur primarily in soil depressions, old riverbeds, or pits left by uprooted trees. Ponds fill quickly after heavy rainfall or when the groundwater table rises during the rainy season (Murphy 2003). Numerous studies document that, during the rainy season, a variety of anuran species uses both peccary wallows and ponds as foraging and breeding habitats (Duellman 2005, Gascon 1991, Zimmerman & Simberloff 1996). Habitat for anurans may become limited when the groundwater table drops and rainfall is less frequent during the dry season (Duellman 2005). If the utilization of wallows by peccaries positively influences hydroperiod but does not affect the water quality (Cameron 2008), wallows could be favourable foraging and breeding habitats for anurans.

In this study, we assessed if peccaries can be classified as ecosystem engineers by investigating whether wallows created and maintained by peccaries are habitats exploited by anuran species. We focused on how wallows affect anurans during the dry season. Specifically we hypothesized that, compared to naturally occurring ponds; peccary wallows will have (1) a longer hydroperiod; (2) similar water quality; (3) greater density of tadpoles, metamorphs and adult anurans; and (4) greater species richness and β -diversity.

METHODS

Study site

We conducted this study at Cocha Cashu Biological Station (11°54'S, 71°22'W), located in the south-eastern Amazonas within Manu National Park, Peru. With over

2 million hectares, Manu National Park represents one of the largest continuous and protected tropical forests in the world (Beck 2008, Terborgh 1990). Because of Manu's pristine setting (i.e. no roads, and only accessible by a 3-day expedition in a boat), and exceptionally large diversity of habitats and species, UNESCO declared Manu as a World Heritage Site in 1987. Cocha Cashu Biological Station is one of the few research sites with both an undisturbed ecosystem and natural populations of both top predators and prey species including collared and white-lipped peccaries (Beck 2008, Terborgh 1990). The station encompasses over 15 km² of forest with more than 60 km of marked trails arranged in a grid system. Yearly rainfall averages 2000 mm with most precipitation occurring from November to May (Terborgh 1990). An average of 100 mm of rain falls during the dry season, from June to October (Terborgh 1990).

Survey of peccary wallows and ponds

Wallows could be distinguished from natural ponds by signs of peccary wallowing activities such as footprints, hair impressions in the mud, or mud spray on the surrounding vegetation. Peccaries visit wallows frequently and the oldest wallows have been used for at least 17 y. As herds of peccaries repeatedly utilize wallows, their activities, primarily trampling, digging and resting, maintain distinct microhabitats within the forest (i.e. no leaf litter and understorey vegetation; Beck 2008, Gascon & Zimmerman 1998). In contrast to wallows, vegetation occurred throughout pond areas and the soil is covered with leaf litter. We chose trails in a manner that allowed us to encounter a variety of soil types and microhabitats. We surveyed a total of 13.7 km of trails from April to November 2004. We extended this surveying to 25 km of trails from June to September 2007, which were re-surveyed between June and July in 2008. To determine the number of peccary wallows and ponds available during the dry seasons, we walked trails monthly and sampled all water bodies within 10 m on either side of the trails.

Hydroperiod of peccary wallows and ponds

At monthly intervals (April–November) in 2004, we estimated surface area by measuring the maximum length and the perpendicular width of standing water in each wallow ($n = 21$) and pond ($n = 13$). Because most water bodies were oval, we calculated surface areas using the formula for an ellipse.

We examined how strongly rainfall affected the hydroperiod of wallows and ponds by applying a linear regression with monthly rainfall as a predictor of mean monthly surface area. In order to test whether hydroperiod differed between wallows and ponds, we

compared monthly mean surface area using a one-way repeated-measures ANOVA. Data were log-transformed to meet the underlying assumption of normality. Finally, we explored if there was a relationship between water area and the total number of anuran species encountered. For each wallow and pond we calculated the mean surface area across the dry season (April–November in 2004) and performed linear regressions using number of species (all three life stages combined) as a dependent variable.

Water quality parameters of peccary wallows and ponds

Physical and chemical water parameters such as pH, dissolved oxygen and temperature can affect the growth and survival of many anuran species (Duellman & Trueb 1994). To explore if wallowing activity affects water parameters, in 2007 (June–September), we measured pH, dissolved oxygen and water temperature in wallows and ponds on a monthly basis using a handheld Oakton pH/DO 300 Meter. To minimize potential bias we randomized the time of data collection for the water bodies. Because the data did not meet the assumptions of normality, we used separate Mann–Whitney U-tests and compared the pooled data across the 3-mo period between water bodies.

Density of anuran species in peccary wallows and ponds

We sampled wallows and ponds for tadpoles, metamorphs and adult anurans monthly during a total of 14 mo across 3 years (2004, 2007 and 2008). Upon arriving at a water body, we searched and captured metamorphs and adults for at least 5 min across the total water surface and 1 m away from the water's edge until no further captures were made. We photographed captured individuals and, when necessary, took voucher specimens for identification and later verification by experts. To sample tadpoles, we dip-netted each water body using a metal strainer and aquarium fish net for at least 5 min or until no further captures occurred. We collected up to four voucher samples of each tadpole morphotype and reared them in the laboratory to facilitate species identification. We calculated monthly mean density of tadpoles, metamorphs and adult anurans in wallows and ponds by estimating monthly mean number of individuals for each water body per unit area of water surface and compared those using a one-way MANOVA. Because the data did not meet the statistical assumptions, we compared monthly numbers of tadpole, metamorph and adult anuran species between wallows and ponds using separate Mann–Whitney U-tests.

Adult species richness and β -diversity in peccary wallows and ponds

Because sample sizes for tadpoles and metamorphs were too small, we focused on adult anurans only. We first

measured similarity of adult anuran β -diversity between water bodies by calculating a Morisita–Horn index with the program ESTIMATE S ver. 8.0 (<http://viceroy.eeb.uconn.edu/estimates>). We chose the Morisita–Horn index because it is unbiased with respect to sample size and richness, and therefore is one of the most robust β -similarity indices (Cramer & Willig 2004, Magurran 2003).

Secondly, we estimated expected adult species richness by pooling the data within each water body and employing sample-based rarefaction statistics using ESTIMATE S. The rarefaction statistics provide an unbiased estimate of expected species richness when sample effort is unequal or when an unequal number of individuals are observed across samples (Colwell & Coddington 1994, Gotelli & Colwell 2001). We randomized the sample order 1000 times without replacement (Gotelli & Colwell 2001) and used the Chao 2 statistic (Chao 1987) to determine expected species richness. Statistical analyses were performed with PASW (2009, Version 17, Chicago, Illinois).

RESULTS

Hydroperiod of peccary wallows and ponds

We located 21 wallows and 13 ponds in 2004 and, after extending our survey area in 2007 and 2008, located a total of 61 wallows and 36 ponds. We found no evidence that peccaries used any pond for wallowing. On only three occasions did we find tapir (*Tapirus terrestris*, Linnaeus) footprints in wallows. We did not encounter faecal matter in wallows or ponds.

During the dry season of 2004, there was a strong positive relationship between monthly rainfall and mean surface area both for peccary wallows ($F = 62.5$, $df = 1, 6$, $r^2 = 0.912$, $P < 0.001$) and ponds ($F = 48.4$, $df = 1, 6$, $r^2 = 0.890$, $P < 0.001$).

Comparison of the hydrology of both water bodies over the course of the dry season in 2004 revealed some striking differences. Over the course of 8 mo peccary wallows had consistently and significantly larger mean water surface areas than did ponds ($F = 158$, $df = 1, 32$, $P < 0.001$, Figure 1). During April and November, the two wettest months sampled with highest rainfall, wallows constituted 80% and 83%, respectively, of the total water surface. During July and September, the two driest months, the surface areas of wallows increased to 89% and 92%, respectively, of the total water surface. On average, wallows were dry for 1.5 mo whereas ponds were dry for 3 mo. Only one wallow was dry for 3 consecutive months, whereas three ponds dried up for 6 mo. There was a strong positive relationship between wallow water surface areas and the total number of anuran species ($F = 32.7$, $df = 1, 20$, $r^2 = 0.634$, $P < 0.001$), but a weaker relationship for ponds ($F = 8.9$, $df = 1, 12$, $r^2 = 0.446$, $P = 0.013$).

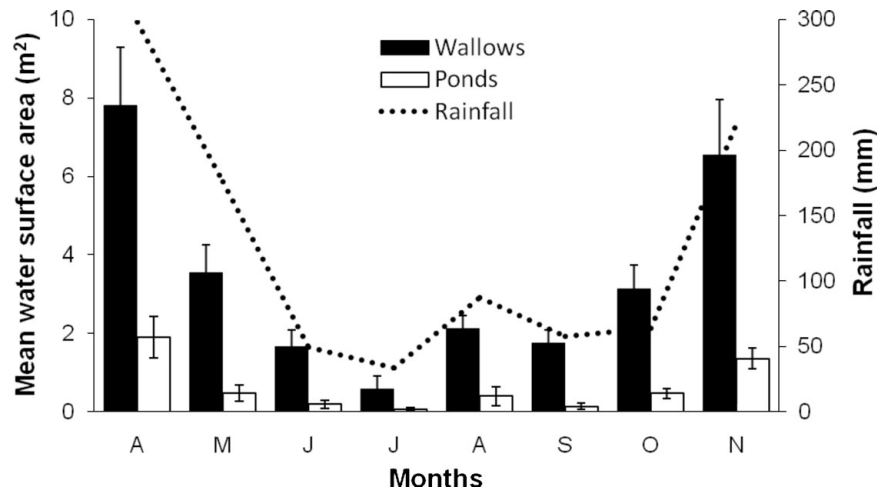


Figure 1. Mean (± 1 SE) water surface area of peccary wallows ($n = 21$) and ponds ($n = 13$) over 8 consecutive months across the entire dry season in 2004, at Cocha Cashu Biological Station, Peru.

Water quality parameters of peccary wallows and ponds

There were no monthly differences in pH ($U = 97.5$, $P = 0.085$), wallows: mean \pm SE = 7.03 ± 0.0 , ponds: 6.76 ± 0.1 ; dissolved oxygen ($U = 88.0$, $P = 0.144$), wallows: $23.5\% \pm 2.4\%$, ponds: $13.2\% \pm 5.5\%$; or water temperature ($U = 112$, $P = 0.117$), wallows: $23.6^\circ\text{C} \pm 0.1^\circ\text{C}$, ponds: $22.5^\circ\text{C} \pm 0.6^\circ\text{C}$ between water bodies.

Density of anuran species in peccary wallows and ponds

Across the dry seasons of three years, the mean monthly density of tadpoles was significantly greater ($F = 45.6$, $df = 2, 26$, $P < 0.001$) in wallows ($2.6 \pm 0.5 \text{ m}^{-2}$) compared with ponds ($0.1 \pm 0.05 \text{ m}^{-2}$, Figure 2a). Similarly, metamorph density was higher ($F = 20.5$, $df = 2, 26$, $P < 0.001$) in wallows ($0.6 \pm 0.1 \text{ m}^{-2}$) than ponds ($0.01 \pm 0.009 \text{ m}^{-2}$). The same was true for per month mean adult anuran density ($F = 36.1$, $df = 2, 26$, $P < 0.001$) when comparing wallows ($1.3 \pm 0.3 \text{ m}^{-2}$) and ponds ($0.1 \pm 0.04 \text{ m}^{-2}$, Figure 2a).

Adult species richness and β -diversity in peccary wallows and ponds

Along transects surveyed over the course of three dry seasons we found tadpoles of a total of nine species in wallows and three species in ponds. Metamorphs of six species occurred in wallows and only one in ponds. While adult anurans of 21 species occurred in wallows, only five species occurred in ponds (Figure 2b, Appendix 1). Overall, we found significantly higher mean monthly numbers of species for tadpoles ($U = 2.00$, $P = 0.009$), wallows: 3.0 ± 0.5 , ponds: 0.5 ± 0.3 ; metamorphs

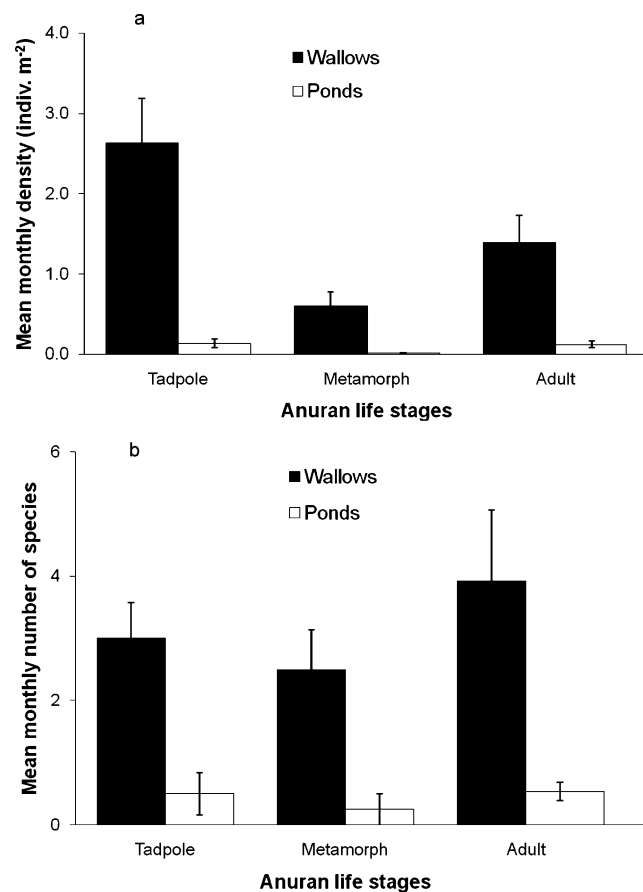


Figure 2. Comparisons of mean (± 1 SE) monthly densities (a) and mean (± 1 SE) monthly number of species (b) for all three anuran life stages in peccary wallows and naturally occurring ponds over the course of 14 mo during three dry seasons at Cocha Cashu Biological Station, Peru.

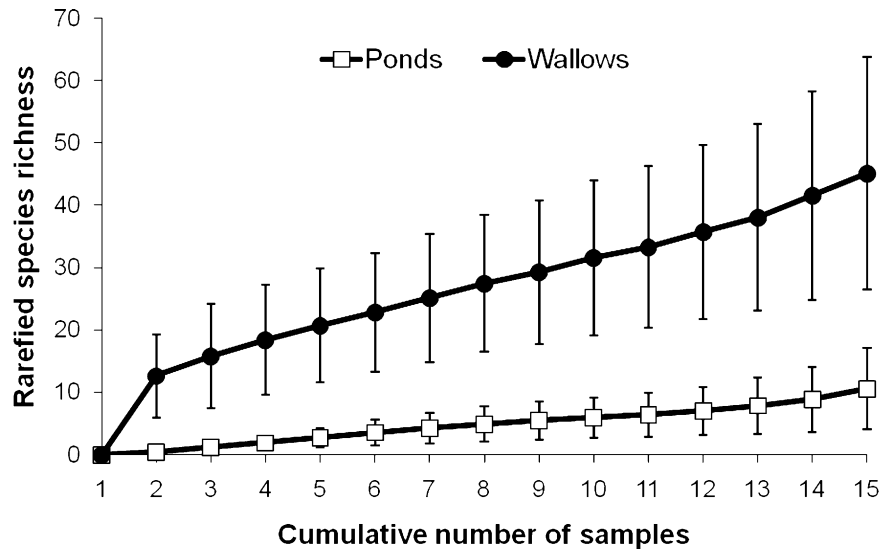


Figure 3. Rarefied species richness (\pm 95% CI) of adult anurans in peccary wallows and ponds over the course of 14 mo during three dry seasons at Cocha Cashu Biological Station, Peru.

($U = 0.50$, $P = 0.029$), wallows: 2.5 ± 0.5 , ponds: 0.2 ± 0.2 ; and adult anurans ($U = 17.5$, $P < 0.001$), wallows: 3.9 ± 1.1 , ponds: 0.5 ± 0.1 in wallows compared with ponds (Figure 2b). Beta diversity of adult anurans (Morisita–Horn index) between the water bodies was 0.34. The rarefaction statistic indicated a difference in the estimated total expected species richness of adult anurans between peccary wallows: 45.1 (95% CI = 6.67–18.7) and ponds: 10.6 (95% CI = 0.0–6.53, Figure 3).

DISCUSSION

The strong significant positive relationships between rainfall and the hydroperiods of both types of water body highlight their dependence on precipitation as the main water source during dry seasons. However, the hydroperiod expressed in mean monthly water surface area of wallows was consistently higher than for ponds. During the 7 mo in 2004, wallows represented between 80% and 92% of the total available water surface area along the 13.7 km transect. As demonstrated in previous studies, peccary activity enlarged and deepened wallows through time and thereby kept them from filling with debris (Cramer & Willig 2004, Gascon & Zimmerman 1998, Simberloff 1992, Zimmerman & Bierregaard 1986). Several wallows at Cocha Cashu have been used for at least 17 y and may be much older. On numerous occasions, we encountered over 31 white-lipped peccaries rolling and resting in wallows. Repeated animal trampling can have major impacts on physical soil parameters, primarily resulting in higher soil compaction, reduced water penetration and lower soil water infiltration (Hamza & Anderson 2005, Kozłowski 1999, Silvia *et al.* 2000, Terashima *et al.* 1999).

Furthermore, the impacts of trampling are higher at elevated soil moisture (Imhoff *et al.* 2000, Scholz & Hennings 1995), a condition found at wallows. One might argue that peccaries removed some water from wallows by splashing, or simply by soaking up water in their pelage and discarding it elsewhere by shaking or evaporation. Nevertheless, the amount of water removal might not be significant because our results confirmed that peccary wallows maintained longer hydroperiods than ponds. Water surface area was also a stronger predictor for the number of anuran species found in wallows than in ponds.

Our findings indicated that peccary activity did not significantly affect pH, dissolved oxygen and temperature in wallows; but all variables were higher in wallows than ponds. Preliminary chemical water analyses of nitrate, phosphate, ammonia and conductivity revealed no differences between water bodies (Cameron 2008). We did not encounter faecal matter in any water body, suggesting that no additional organic matter was added that might have changed its chemical and microbial composition. Compared with ponds, the trampling and soil disturbance clearly reduced leaf litter and understorey vegetation in wallows. Differences in leaf litter decomposition might affect dissolved organic carbon and the microbial communities, but apparently did not affect water quality in wallows.

Over three dry seasons we found higher densities of all three anuran life stages in peccary wallows than in naturally formed ponds. Greater mean densities of tadpoles and metamorphs may indicate that anurans have higher reproductive activities in the more hydrologically stable wallows compared with the ephemeral ponds.

Monthly number of species of all three anuran life stages was also higher in wallows than ponds. We found tadpoles of six out of nine anuran species, six metamorphs out of seven anuran species, and adults of 17 out of 22 anuran species occurred only in peccary wallows. A small overlap of anuran species found as adults between water bodies was also evident by the low Morisita–Horn index (0.34). The number of adult anurans and estimated species richness were both higher for wallows. The non-asymptotic nature of the rarefaction curves suggests that continuing sampling would further increase the number of species, especially for wallows. However, the non-overlapping 95% CI indicates a difference in species richness. The fact that ponds dried up faster than wallows may explain why we found higher anuran density and species richness in peccary wallows (Cameron 2008, Gascon 1991, 1995; Zimmerman & Bierregaard 1986, Zimmerman & Simberloff 1996).

A few previous studies investigated anuran communities in peccary wallows; however, all were conducted during rainy seasons when other water bodies were also available (Gascon 1991, 1992, 1995; Zimmerman & Simberloff 1996). Nevertheless, their findings parallel ours. For instance, in Brazil, Gascon (1991) found a significantly higher mean number of anuran species in peccary wallows (5.5) compared with ponds (4.8). Furthermore, tadpole density of the four most common anuran species was significantly higher in peccary wallows than ponds (Gascon 1995). Other studies encountered up to seven anuran species breeding exclusively in wallows during the rainy season (Zimmerman & Bierregaard 1986, Zimmerman & Simberloff 1996). The last two studies were carried out in experimentally fragmented forests, ranging in size from 10 to 500 ha, and contained only the collared peccary at the beginning of the experiment. The more gregarious white-lipped peccary was already locally extinct. Once the collared peccary vanished from these fragments, several anuran species had reduced abundance and some went locally extinct (Zimmerman & Bierregaard 1986). A number of studies linked the local decline or extinction of numerous anuran species with the disappearance of peccaries and their wallows as breeding habitats (Laurance *et al.* 2002, Simberloff 1992, Zimmerman & Bierregaard 1986). Consequently, we could infer that peccary wallows are crucial breeding habitats for several anuran species, even during the rainy season. Wallows may maintain anuran population densities and species richness, not only by providing critical water resources for rehydration and foraging habitat, but also by acting as stepping stones through the forest, thereby increasing dispersal distance and genetic diversity (Duellman 2005, Marsh *et al.* 1999). We found that understorey vegetation, including seedlings and saplings, grows in and at the vicinity of ponds. Conversely, this is not the case at

wallows. Trampling and wallowing activities destroy vegetation (see also Gascon & Zimmerman 1998) and thereby can have negative effects on plant recruitment and distributions.

In conclusion, this was the first study to systematically contrast the hydroperiods, water parameters, anuran density and species richness across dry seasons between peccary wallows and ponds within an intact ecosystem where both species of peccary occur at natural densities. The results indicate that peccaries maintain and alter the hydroperiods of wallows thus making a limited resource available to anurans. Wallows function as aquatic habitats that support increased anuran density, β -diversity and species richness. Therefore, by definition peccaries can be considered ecosystem engineers. These findings are also important for conservation and management. Habitat destruction and overhunting have increased local and regional extinctions of peccaries throughout their geographic range (Beck 2005, 2008; Taber *et al.* 2008). Studies demonstrated that their extinction resulted in the eliminations of critical non-redundant trophic interactions (e.g. seed predation and dispersal; Beck 2005, 2006), and non-trophic species interactions (Beck 2008, Gascon & Zimmerman 1998, Zimmerman & Bierregaard 1986). Both trophic and non-trophic interactions of peccary with other species contribute and maintain Neotropical forest structure and species diversity (Beck 2005, 2006; Gascon & Zimmerman 1998, Taber *et al.* 2008).

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Appendix 1. Life stages and anuran species found in 36 ponds (P) and 61 wallows (W) during dry seasons in 2004, 2007 and 2008 in Cocha Cashu Biological Station, Peru.

Anuran species	Tadpole	Metamorph	Adult
<i>Adenomera andreae</i> Müller	P & W	W	P & W
<i>Allobates femoralis</i> (Boulenger)			W
<i>Bufo marinus</i> (Linnaeus)			W
<i>Chiasmocleis ventrimaculata</i> (Andersson)	W		W
<i>Colostethus trilineatus</i> (Boulenger)			W
<i>Colostethus marchesianus</i> Melin	W		W
<i>Edalorhina perezi</i> Espada	P & W	W	P & W
<i>Elachistocleis bicolor</i> Guérin-Méneville			W
<i>Eleutherodactylus fenestratus</i> (Steindachner)			P
<i>Eleutherodactylus skydmainos</i> Flores & Rodríguez			P & W
<i>Epidobates</i> sp.			W
<i>Hamptophryne boliviana</i> (Parker)			W
<i>Hyla leucophyllata</i> Bereis	W		
<i>Hyla lanciformis</i> Cope	W		
<i>Hyla punctata</i> (Schneider)	P & W	P	
<i>Hyla</i> sp.	W		P & W
<i>Leptodactylus didymus</i> Heyer, Garcia-Lopez & Cardoso			W
<i>Leptodactylus leptodactyloide</i> (Andersson)		W	W
<i>Leptodactylus mystaceus</i> Spix			W
<i>Leptodactylus petersii</i> (Steindachner)		W	W
<i>Leptodactylus rhodonotus</i> (Günther)			W
<i>Phyllomedusa palliata</i> Peters			W
<i>Phyllomedusa tomopterna</i> (Cope)	W		W
<i>Physalaemus petersi</i> (Espada)		W	W
<i>Sphaenorhynchus dorisae</i> Goin			W
<i>Scinax</i> sp.		W	