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Ethnographic Observations on the Role of Domestic Dogs in the Lowland Tropics of Belize with Emphasis on Crop Protection and Subsistence Hunting

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Abstract

We report functional relationships between humans and canines based on observations in the village of Santa Cruz (Toledo District, Belize), emphasizing the cultural ecology of dogs in this lowland tropical rainforest setting and milpa agriculture subsistence system. Dogs pursue animals threatening field crops; they deter forest herbivores by leaving their scent along the myriad trails from the village to the milpa field plots; and they guard the homestead and foods stored there. Dogs also aid in daytime hunts for species that can be cornered. They are less useful in pursuits of fast species like deer and are protected from pursuing especially dangerous species like anteater or warri. Litter survival rates are low, and the lifespan of hunting dogs is significantly shorter than that of guard dogs due to hazards of forest pursuit. Explicit training for hunting is limited and maintenance costs are low as dogs are fed a partial ration of tortillas and otherwise scavenge for their diet. The village population of dogs appears not to be under genetic selection for hunting skills. Our results advance the comparative ethnographic study of this important domesticate; they should aid in the formulation and assessment of hypotheses about dog domestication and co-evolution with human society.

Keywords Cultural ecology · Hunting · Guarding · Canine domestication · Tropical lowland rainforest · Milpa agriculture · Mopan Maya · Santa Cruz village · Toledo District · Belize

Introduction

We present a canine ethnography in a contemporary society subsisting on milpa agriculture in a tropical lowland setting. Following a cultural ecology approach, we report dog–human functional relationships in terms of their costs and benefits. We draw on interviews, surveys, and participant observation. Previous studies have referenced hunting with dogs in southern Belize (Doherty 2005; Zarger 2002), however none have provided detailed, quantitative

ethnographic observations. In a subsequent study we analyze human–dog coordinated movements based on GPS-tracking and focal-follow records of actual hunts.

Examination of canine functions in societies described ethnographically as well as those inferred from archaeological evidence has generated multiple possible motives for the domestication and community maintenance of village dogs, including companionship, hunting support, and transportation (Manwell and Baker 1984). Humans also might have found valuable dogs' behavioral flexibility and cooperation during niche and geographic expansions in the late Pleistocene/Holocene (Bleed 2006). Dog remains consistently appear in human archeological settings associated with the advent of agriculture (Lupo 2019). Despite the value of ethnographic insights for analysis of canine domestication and their ongoing commensalism with humans, dogs, like children (Hewlett 2014), are sometimes invisible in ethnography even if present and consequential in human communities. Our analyses aim to advance the comparative ethnography of this important domesticate and inform hypotheses about

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Fig. 1 Location of Santa Cruz. Longitude and latitude (decimal degrees) are shown on the bottom and left sides of the frame. Map compiled using QGIS (QGIS Development Team 2019)

canine benefits and costs in a manner that contributes to understanding of their domestication.

Study Site

Environment and geography

Santa Cruz village is in the uplands of Toledo District (16.2406° N, -89.0703° W; 265 m asl; Fig. 1), a region of fertile hilly relief. Community lands spread to the east and northeast of the Rio Blanco, the Moho River watershed, and to the north of a karstic ridge locally known as The Rock Patch (Culleton 2012; Supreme Court of Belize 2007). As categorized by Olson et al. (2001), Santa Cruz belongs to a ‘Tropical and subtropical moist broadleaf forests’ biome, more specifically to the ‘Petén-Veracruz moist forests’ ecoregion. Annual precipitation during April 2012 to March 2013 was 2449 mm (HOBO U30 Station).

Vegetation in and surrounding the community of Santa Cruz is a mixture of agricultural fields, secondary forest patches in various stages of succession, and primary forest

that is located about an hour’s walk (2 km) from the village. The natural vegetation is highly diverse in fertile and well drained areas. Trees include ceiba (*Ceiba pentandra*), cohune palm (*Attalea cohune*), quamwood (*Schizolobium parahyba*), madre cacao (*Gliricidia sepium*), mahogany (*Swietenia macrophylla*), and cedar (*Cedrela odorata*) (King et al. 1986; Standley and Record 1936; Wilk 1997; for further details of vegetation types and trees see Hartshorn et al. 1984; for a list of plants with edible or other uses see Zarger 2002 and Baines 2012).

Present-day Santa Cruz

Santa Cruz has 82 households, 428 residents (207 male, and 221 female), and 148 adult dogs, as many dogs as children aged 13 and under (Atwater et al. 2012). Dogs guard household property and fields. In some households they offer affection as pets although they occasionally kill valuable chickens or piglets. They also aid villagers in the quest for game in the forests surrounding the village and its patchwork hinterland of agricultural fields mixed with forest regrowth,

helping to provide animal protein in a diet otherwise centered on maize agriculture.

Most Santa Cruz households cultivate maize and associated crops using the slash-and-burn system. Cortez (2016) provides a detailed account of residents' strategies for managing their milpa and matahambre¹ fields. Men can provide additional household income in cash by marketing maize, occasionally rice or cacao, or by formal wage labor performed for the NSF #0827277 project's archaeologists, construction projects, or patrons representing firms from outside the village. Women are responsible for meal preparation, household hygiene, and childcare; some sporadically sell jippi-jappa (*Carludovica palmata*) handicrafts to visiting tourists.

Most Santa Cruz residents speak Mopan Maya, while a few speak Kekchi (Q'eqchi') or Spanish at home. The men speak English for commercial or official transactions outside the village. Goods like coffee, sugar, flour or textiles, and dogs can be purchased at Punta Gorda, Toledo's capital, located 43 km to the southeast. Supplies like machetes, plastic goods, agro-chemicals, or ritual costumes and musical instruments can also be acquired or rented at Santa Cruz Frontera (Guatemala) 20 km to the east on the road to Jalacté (see Supplemental Materials (SM) "Sect. 1: Prehistory and History" for a brief historical overview of Santa Cruz).

Methods

The fieldwork reported here was conducted over 13 months (June–July 2011 and January–December 2012) by LPC who with his wife and young son were living in the community (see SM "Sect. 2: Permissions"). Tuli (Fig. 2a), a dog associated with the thatch house built for the project's series of ethnographers, became a companion to LPC during visits to households and on farming and hunting trips. Our results draw on (a) general participant observation and informal interviews (Notes); (b) periodic semi-structured interviews on hunting allocation efforts (HA); (c) a formal village-wide household demographic survey (HDS); and, (d) focal-follow of hunting trips tracked with GPS and heart rate devices (GPS/HR). Data on the household distribution of dogs by sex, age, and pup survival, as well as life expectancy estimates, come from responses to questions included on the project's demographic and economic survey (HDS). To learn about the functional roles that households assign canines, we draw on observations made while visiting households (Notes) or joining trips to the farms (GPS/HR), along with conversations with randomly selected hunters every sixth day (HA). Further details on dogs' functional roles,

¹ Maize intercropped with *Mucuna* spp. beans.

types, origin, breeding, feeding, training, and medical care expenses are drawn from HDS and general participant observation (see SM "Sect. 3: Field Methods").

Evidence on subsistence hunting was gathered through all our methods and provides insights into: the frequency and duration (hours) of trips, time of the day, the presence and roles of dogs, risk and injuries, training, prey harvests (kg), and canid-human configurations of the hunting parties. We counted a trip as successful if game was harvested (kg > 0); if more than one capture occurred per trip we summed individual weights and report the total harvest. When possible, we weighed (kg) captured game, otherwise we registered hunters' best estimate (see SM, "Sect. 4: Reported Versus Measured Weights of Resources," for estimates of the accuracy of this procedure). When local game species data were unavailable, we used average prey weights from Koster (2008a) and Primack (1997).

We focus our analysis on the 76 households (of 82 in the community) for which we were able to complete the HDS. We use hunting frequency reported by households (HDS) in combination with total hunting episodes recorded (Notes, HA, GPS/HR) to classify households as 'active hunters,' 'occasional hunters,' 'past hunters,' or 'non-hunters.' For data management and analyses we used R (2020). The raw data and analysis code is maintained at <https://www.github.com/PacheCoLuis/ethnodogs>.

Results

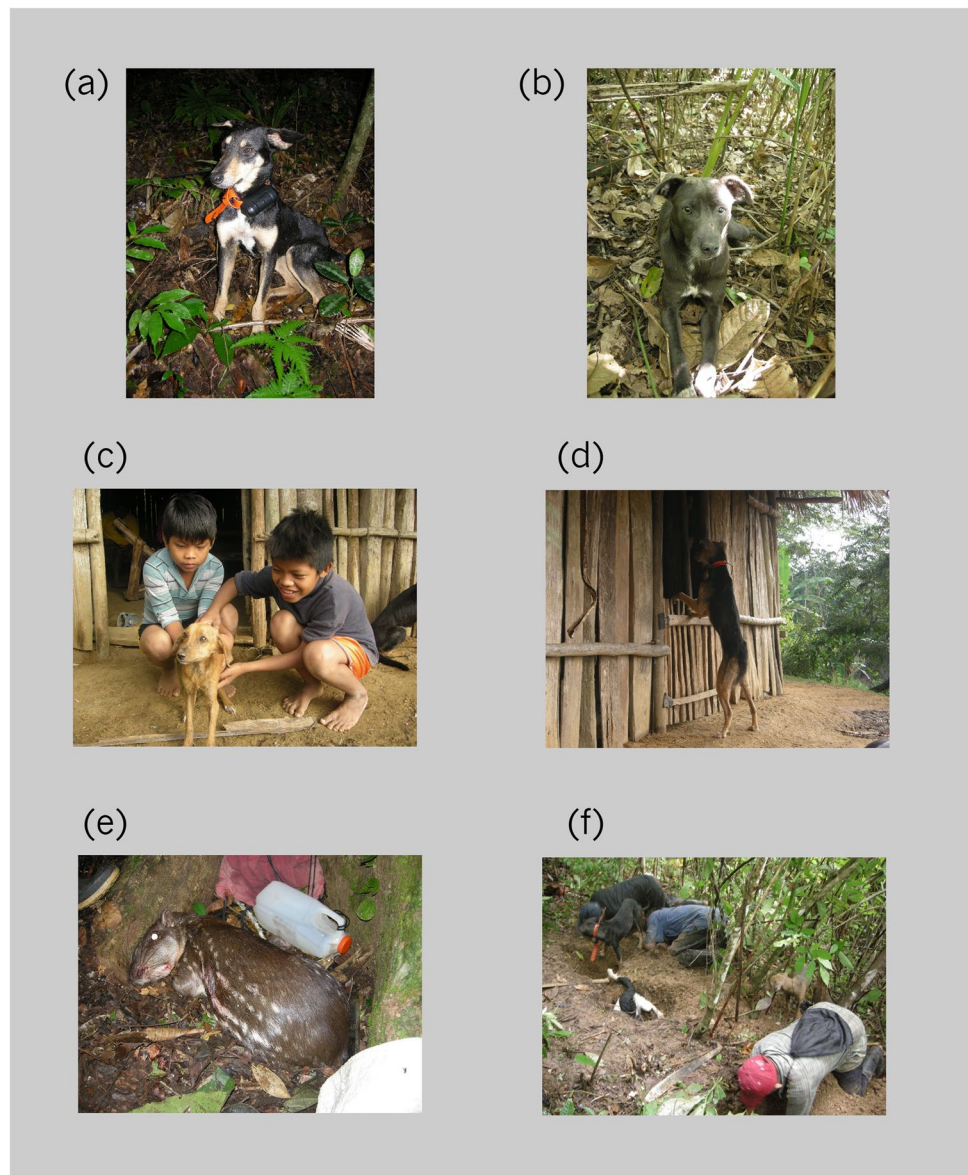
Classification of households

Household hunting effort is distributed as follows: 1) active hunters (n = 17), participating in 0.5 to 5.6 hunting trips per month; 2) occasional hunters (n = 24), participating in 0.1 to 0.4 hunting trips per month; 3) past hunters (n = 18), household heads reporting active or occasional hunting in the past but not at present; and 4) non-hunters (n = 17), households reporting no past or present hunting.

Demography of dogs

In 2012 there were 77 male and 71 female adult dogs associated with 55 (72%) of the surveyed households (Table 1). Households usually keep one to four dogs (Fig. S1). More than half (n = 33; 60%) of the surveyed dog-owning households experienced a litter over the previous 12 months. Of 143 pups born 114 died, a survival rate of 20%. Litters from 49 females have an average size of 4.3 puppies of which 3.5 die within a year. Interviewees reported 23 adult dog deaths in the six months prior to survey administration, an annual adult survival rate of 69%. Adult dog mortality increased

Fig. 2 Maya dogs and hunting scenarios in Santa Cruz village a) Tuli, the project's Maya peck dog; b) a skilled hunting dog; c) the smallest hunting dog; d) the biggest hunting dog; e) a nocturnal hunt without dogs and capture of a gibnut; and f) a day hunt with dogs, all members of the party trying to dig-out an agouti. The dogs in a), d) and f) are wearing orange DC40 radio-tracking GPS collars



near the end of fieldwork as some animals living in households next to a new highway were hit by motor vehicles.

The reported life expectancy of dogs differs according to their primary function. Interviewees expect guard dogs surviving the puppy stage to live 6.6 years ($n = 23$ households reporting) and hunting dogs to live 3.7 years ($n = 44$; Fig. 3; t-test for difference of means significant at the 0.001 level, $t = 4.9$, $df = 43.5$, 95 PCI: 1.7, 4) (see SM “Sect. 5: Canine Lifespan in Relation to Size” for details on reported lifespans we treat as outliers). Although all female dog types have litters, guard and uncategorized females (25 with pups out of 31) are associated with most pups born ($n = 80$) and an average pup:female ratio of 3.2, while female hunters (24 with pups out of 40) are associated with fewer pups born ($n = 67$) and an average

pup:female ratio of 2.8. Some owners castrate their male dogs to prevent them from bothersome wandering and fighting over estrus females. They appear not to view this as a population control tactic.

Breeding for particular traits is not an intentional practice of villagers. The locally recognized default breed is the *Maya peck* (dog), described by a native speaker after looking at the project dog, Tuli (Fig. 2a). While we did not make morphometric measures, we can provide approximate sizes of Santa Cruz dogs based on photographic records. Most dogs are about 55 cm in height, measured at the shoulder (range 40 to 70 cm, Fig. 2c-d) and weigh between 7 and 18 kg (15 to 40 lbs). In general, hunting dogs (Fig. 2b-d) are more ectomorphic than guard dogs.

Table 1 Household distribution of dogs by sex and age, as reported for the previous 12 months

	HOUSEHOLDS	ADULT DOGS	PUPS BORN/ OWNED ¹
SEX			
Male adult dogs only	15	24	17
Female adult dogs only	14	24	58
Both (M+F=Sum)	26	53+47=100	68
Total (M+F=Sum)	55	77+71=148	143
AGE			
Adult dogs only (M+F=Sum)	22	38+22=60	0
Puppies only	1	0	4
Adults & Pups (M+F=Sum)	33	39+49=88	29 ²
Total (M+F=Sum)	56 ³	77+71=148	

¹We did not record the sex of pups, only the total number in households reporting that they possessed puppies in the 12 months previous to the survey

²This is a count of surviving pups only

³The additional case (n=55+1) in the distribution of dogs by age includes the one “puppies only” household

Functions and maintenance of dogs

An elder hunter stated that “dogs can do a lot of work:” they go to the farm, guard fields, hunt, guard houses, and can even be trained to transport firewood. These, in addition to affection and companionship, were the only uses of dogs observed in Santa Cruz.

Functions

At home, dogs announce the approach of visitors, receive food and care, and can shelter under the thatch-roof awnings. Owners use their dogs either as household guards (n=13 households; 28 dogs) or as hunters (n=23 households; 86 dogs); the balance of 19 households with 34 dogs did not assign or would not choose a category (Table 2, minor discrepancies between household counts are due to missing data in some cells). Hunting dogs adopt the guard role at home; guard dogs, however, do not join trips to the milpa fields or participate in hunting. Hunting dogs acting as guards may threaten or bite visitors, although if at home the alerted owner can control his/her dogs.

At the farm, dogs act as human companions and as sentries alert for crop-damaging herbivores. Joining their owners on daily trips to and from milpa plots, dogs mark their passage by leaving their scent along the network of trails interlaced among the cultivated fields. Hunters state that the dogs’ odors linger for a few days as a deterrent to

agricultural pests. In this manner, the dogs provide protection even to community members who do not own them. When dogs detect herbivore pests, they chase them from milpa area whether or not the sighting initiates a hunting pursuit.

Maintenance

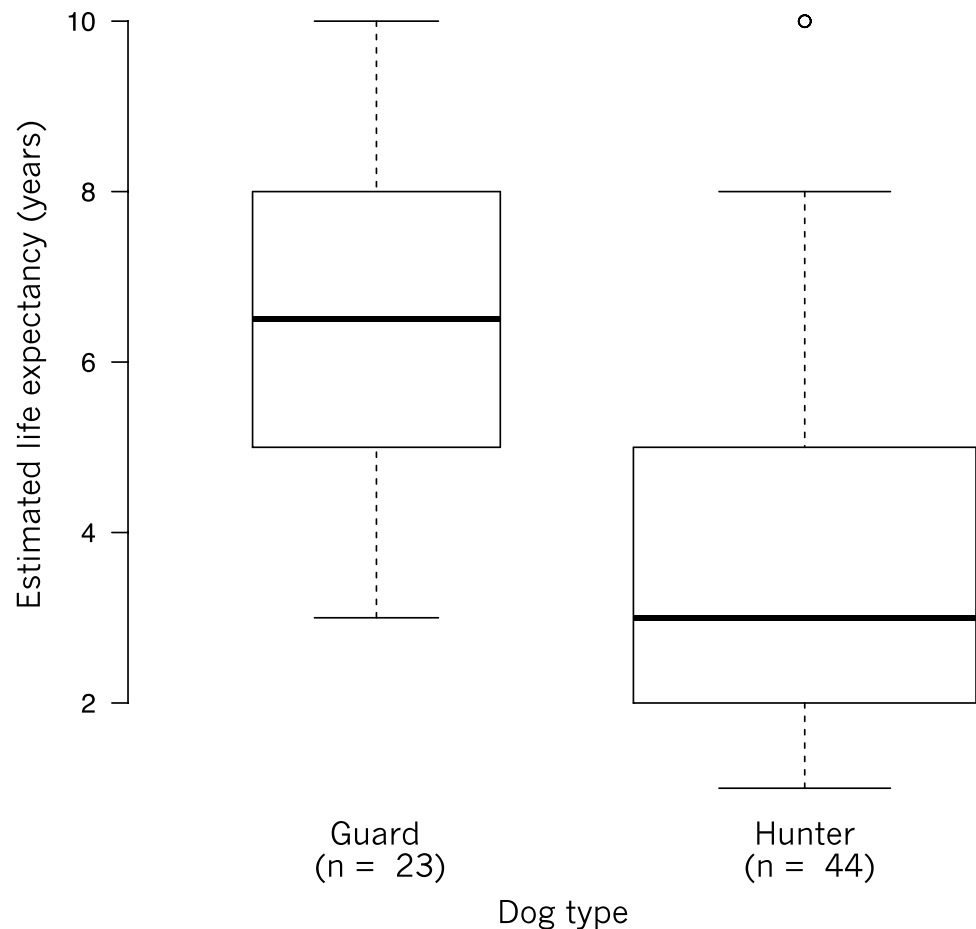
Training: experienced hunters intentionally avoid handling their young dogs or feeding their adult dogs before hunting, stating this keeps them wild, ensuring that they will more readily chase game. Hunters expose their dogs to diverse hunting situations, preferring not to train them to hunt a specific animal. This allows hunters to assess whether a particular dog is inclined to hunt and which prey they themselves prefer to pursue. Youths who also are just learning to hunt often have closer contact with their dogs, establishing bonds of affection by petting them (Fig. 2c).

Hunters start to observe and assess a dog’s hunting aptitude as soon as it is able to follow them to the fields, usually at about three months of age. Some pups are inclined to stay at the household; others are keen to join daily subsistence activities. Hunters do not insist on a dog’s participation in hunting, but they encourage pups that show motivation to do so, distinguishing among dogs that like to hunt from those that are lazy (*sakan*). Most respondents (n=24) indicate that dogs also develop or have preferred roles within a hunting pack. A few (n=7) say that you can train dogs to prefer a specific prey and one respondent said that both endogenous and trained prey preferences can develop. Respondents (n=29) estimate that acquiring hunting skills requires about three months (82 days). According to hunters, preparation consists of encouraging promising behaviors that emerge spontaneously or are learned from watching how other hunting dogs behave. Explicit training is limited, although hunters may help young dogs identify the scent of animals by exposing puppies to the prey odor and by allowing all dogs in a party to lick the blood of a capture.

Among their mature hunting dogs, hunters distinguish between guide (*chabe*) and runner (*alca*), *ajch'a'-bej* and *aj'alca'*, respectively, following Hoffing’s (2011) spelling. Guide dogs start the chase and they lead runner dogs through the forest. Active hunters (n=12) hold most guide (10 male, 9 female) and runner (14 male, 6 female) dogs, a proportion that drops to guide (5, 6) and runner (7, 5) dogs with occasional hunters (n=5), and to guide (7, 2) and runner (6, 5) dogs with past hunters (n=6). We did not observe preferential treatment or rewards directed to either type nor did we inquire if hunters made deliberate decisions about the composition of their hunting packs.

While LPC did not train the project dog, Tuli, early on she “attempted to demonstrate her hunting prowess on piglets belonging to [...] neighbors” (Baines 2012:57).

Fig. 3 Estimates of life expectancy for guard and hunting dogs that survive to adulthood. Whiskered boxplots show the medians (bold bars), interquartile ranges (upper and lower limits of boxes, and the whiskers), as well as outliers segregated using standard conventions (small circles). The width of boxplots is scaled by the square root of the number of observations (R Core Team 2020). The sample sizes (n) represent the total number of households reporting age estimates for each dog type. Data source HDS; we omit from the sample ten outliers for which households reported life expectancies above 12 and up to 25 years, as dogs rarely live that long (see SM, Sect. 5). Eliminating these unusually high estimates has no effect on the general magnitude of the difference between guard and hunting dog lifespan



As a suspect in several inconvenient poultry deaths, Tuli's skills continued to develop. She eventually facilitated LPC's research by joining him in focal follows (GPS/HR) of indigenous hunters and their dogs. Her preferred prey was agouti. If she became lost chasing prey, LPC howled to her and she would use the call to reorient and join him. Tuli gradually learned on her own how to coordinate her chasing efforts with humans and dogs from different hunting parties.

Dogs rarely are sold within the village ($n=7$, in the six months prior to the survey). Active hunters rear their dogs from pups rather than buy them as adults (Table 2) whereas occasional hunters are more evenly divided on their preferred source. Past hunters and non-hunters show a more decided preference for raising pups from their household litters. Hunters who buy dogs typically procure them from outside the village, Punta Gorda being a popular source. They pay from \$5 BZD (\$2.5 USD) for a puppy to \$15 BZD for a young or adult dog.

Owners in all household types feed their dogs daily about five tortillas (20 cm in diameter; Table 2). Some hunters, however, reported that they feed their dogs five of a larger tortilla called *pixtun* (25 cm in diameter). Only two of 55 households buy commercial dog food. Dogs also are fed

leftovers, if there are any, and whenever a hen or rooster is killed for household consumption dogs are given the offal and bones. Hunters likewise give their dogs the cleaned bones of captured game. Dogs also get offal and bones from the pigs and chickens prepared for festivities accompanying reciprocal labor exchanges. Canids scavenge in the vicinity of their own and neighboring houses and, if unattended, they will either steal food in kitchens or kill wandering poultry or piglets. Owners discipline such behavior with physical punishment or by tying them up.

A majority (75%) of active hunters report giving medicines such as antibiotics to their puppies or wounded dogs, a level of care that drops to 29% among past hunters, 17% among occasional hunters, and 0% among non-hunters (Table 2). The cost of a single antibiotic injection is \$2.5 BZD; a bulk bottle containing ten injections costs \$5 BZD. Of the ten households reporting an antibiotic expenditure, nine were treating injured hunting dogs. The cost of an anti-parasite treatment is between \$3 and \$4 BZD. Slightly less than half of the households owning dogs reported that the Belizean Department of Agriculture delivers free rabies vaccines; the remainder were either unaware of this service or did not consider it relevant or useful information. Across households, 71% of active hunters acquire the rabies

Table 2 Origin, functions, costs of keeping adult dogs, and distribution of litters by household type

		HOUSEHOLD TYPE				Total
		<i>Active hunters</i>	<i>Occasional hunters</i>	<i>Past hunters</i>	<i>Non-hunters</i>	
SOURCE ¹	Buy	5	8	2	1	16
	Home-born	7	7	11	6	31
	Both	2	2	0	1	5
	Other	2	0	1	1	4
FUNCTION ²	Guard	2 (<i>I+I</i>)	4 (<i>5+2</i>)	3 (<i>2+4</i>)	4 (<i>5+8</i>)	13 (<i>13+15</i>)
	Hunter	15 (<i>25+23</i>)	6 (<i>13+10</i>)	1 (<i>5+5</i>)	1 (<i>2+1</i>)	23 (<i>45+39</i>)
	Both	0	1 (<i>I+I</i>)	0	0	1 (<i>I+I</i>)
	Uncategorized	0	6 (<i>6+4</i>)	9 (<i>10+8</i>)	4 (<i>2+4</i>)	19 (<i>18+16</i>)
COST	Daily tortilla ration	7±7	5±4	4±2	5±4	
	Medicine given Y/N	12/4	3/15	4/10	0/9	19/38
	Vaccine given Y/N	10/4	6/12	9/5	6/3	31/24
ADULTS	Present/absent	16/1	17/7	13/5	9/8	55/21
	Number (M + F = Sum)	26 + 24 = 50	25 + 17 = 42	17 + 17 = 34	9 + 13 = 22	77 + 71 = 148
LITTERS ³	Present/absent	10/7	10/13	7/11	7/9	34/40
	Pups (Born—Died = Alive)	42—30 = 12	52—45 = 7	23—18 = 5	30—25 = 5	147—118 = 29

Throughout, regular font numerals are counts of households, italics are counts of dogs

¹Source of obtaining dogs

²Parenthetical dog counts differentiate males and females (M+F)

³Litters refer to the previous 12 months; pups alive are those surviving from births in the 12 month period prior to the time of the survey (HDS). The four additional born pups tallied here (n = 147) come from the “puppies only” household shown in Table 1

vaccine, which drops to 67% of non-hunters, 64% of past hunters, and 33% of occasional hunters (Table 2).

The burial of a female dog that did not return home from a farm trip and was later found dead in the bush as a consequence of snakebite or dehydration took place during the fieldwork period. The owner brought the body back to the village for an afternoon burial attended by the whole family, weeping over their loss of an excellent hunting dog and companion. A second burial, this time in the bush, was reported by a hunter whose dog was killed by a jaguar.

Subsistence hunting

Hunting trips can either be opportunistic or planned. Villagers engaged in agricultural tasks decide to join their dogs' chases only if they judge the prey worth the effort.

Hunting Frequency

Our ethnographic observations (Notes, HA, GPS/HR) differ somewhat from household heads' responses to questions (HDS) about the frequency of their hunts per month and whether or not they hunt with dogs. Active hunters (88% response) report hunting 1.6 to 16 times/month, while occasional hunters (54% response) report hunting 0.2 to 12 times/month. We do not have observational data on past hunters,

but they (61% response) report hunting 2 to 28 times/month, with four individuals claiming to have hunted every day. Past hunters' upper limit would double, in 13 months, our total observed count of village hunting trips (n = 185, Table 3). The equivalent upper limit for active hunters or occasional hunters is 23 trips above or 29 trips below our total count, respectively, not a large divergence. Dogs are present in 143 of the 185 trips, 3.4 times more frequently than they are absent (42 trips) in our sample (Table 3).

Time and tactics

Diurnal hunts with and without dogs comprise 82% (n = 152; Table 3) of our observational data. Dogs are

Table 3 Hunting sample characteristics by sampling method.

Source	With dogs		Without dogs		Totals
	Day	Night	Day	Night	
Notes	24 (39)	(0)	1 (5)	5 (09)	30 (53)
HA	49 (64)	(0)	2 (3)	4 (17)	55 (84)
GPS/HR	11 (40)	(0)	1 (1)	1 (07)	13 (48)
Totals	84 (143)	(0)	4 (9)	10 (33)	98 (185)

Key. Successful and (Total) number of unique hunting trip records, parsed by presence or absence of dogs, whether diurnal or nocturnal, and by method of data acquisition: general participant observation and informal interviews; HA Hunt Allocation study, GPS/HR opportunistic focal-follow with GPS-tracking

always encouraged to join day hunts and they generally do so unless fatigued or injured. Hunters may plan to hunt alone or together with family members or friends. Residents not willing to chase mammalian pests damaging their crops may solicit the services of a skilled hunter and his dogs. Hunters receive no remuneration for such services, apart from the opportunity to initiate a hunt and perhaps secure game based on recent evidence of its activity and movements. Neither do non-hunters expect compensation for providing an opportunity to hunt in or from their fields.

The morning hike into the fields for agricultural work usually starts around 6:00 AM and can turn into a hunt at any moment. As soon as hunters start dressing, sharpening their machetes or reaching for their guns, household hunting dogs are alert and ready to join them. Hunters use their trail time to check for evidence of overnight activity by game animals. Chases can start abruptly, as hunters and dogs are alerted to any evidence of prey once they leave the village. Tracks, feces, partially eaten fruits, scratched trunks or browsed vegetation are common signs; dogs may also initiate a chase based on scent. Hunters, once they identify an animal trail or footprint, may cue their dogs to seek the animal associated with the evidence.

Dogs bark during a chase, alerting hunters to their position and disposition and hunters howl encouragement to them. Once on a scent, dogs use their agility and smaller size to move quickly through the brushy secondary forest growth. Based on their experience, on interpretation of the evidence that initiated the chase, and on reading of clues from the pace, direction, and barking of their dogs, hunters decide whether to join in or wait. Dogs generally bark in sharp, rapid cries when they corner prey. If hunting as part of a group, hunters may split up in order to surround prey like peccary. Some members of the party might start at faster pace through the bush, while others may adopt a slower pace and keep to known trails.

Planned hunts may entail several days of monitoring and studying prey movement patterns, again typically while walking to and from farm fields. Hunters take note of the direction in which game is moving, to the condition of the animal revealed by its tracks, as well as the time of day the prints were made. As an animal's behavioral profile becomes clear, hunters decide their tactics, for instance, the route each of them will follow to drive prey such as peccaries towards the place where a designated hunter with the shotgun will be waiting.

Daytime hunts can be disrupted by a number of factors: rainfall heavy enough to compromise the ability of dogs and humans to hear one another; confusion generated by overlap between groups of different hunters and their dogs during chases; and prey that are able to escape through undetected burrow exits, outpace the dogs, or evade their pursuers by crossing through running water.

Night-time hunts, which constitute 18% ($n = 33$; Table 3) of our sample, occur without dogs. Hunters report that dogs are left behind to prevent accidental injuries from gun fire and other hazards of chases in the dark. Hunters plan night hunts around moon phase, rise, and set, seeking low-level lunar illumination for safe travel but darker nighttime periods for successful encounters at the chosen hunting spot (SM "Sect. 6: Night-Hunting Preparations"). Overnight hunting trips take place at locations distant from the village where human disturbance is less and encounters with prey more likely; they are special occasions for which hunters prepare by taking 4–10 cartridges.

The largest species hunted, the warri, is pursued during the day without dogs. Hunters report that this animal is ferocious and that its large, sharp incisors can kill dogs. Nevertheless, once they have located and surrounded a warri group, the hunters shout loud imitations of dog barks, hoping to confuse their prey and increase their chances of taking it. Half of the deer hunts and one third of the gibnut (Fig. 2e) hunts occur during night ambushes and thus were without dogs. Collaboration with dogs is focused on prey such as agouti (Fig. 2f), armadillo, and peccary, which are less dangerous and are pursued during daylight hours.²

Risk and injuries

Not every villager is keen to pursue species like peccaries, which run fast through thick secondary forests (*k'ato'k*), elevating the risk of injury both to the hunter and especially to dogs. Household heads (sample of 18) report that dogs are injured during hunting trips (average rate) once every two months/household. Hunters commonly allow wounded dogs to recover before engaging them in hunting again, although we observed incompletely healed dogs join hunters leaving the village. Hunting wounds can cause death or disability, a reality reflected in the shorter reported life span of hunting dogs. Even in cases of long-term or permanent disability some dogs adapt and continue to hunt. A female dog slowed down by a fracture that left her lame nonetheless remained a very skilled hunter of armadillo.

Size of hunting party, harvests, and durations

Drawing on our HA and GPS/HR samples, when hunting with dogs the parties average three hunters and five dogs

² In the SM, "Sect. 7: Prey-Specific Tactics, and Prey," we briefly describe techniques used for individual species, the attenuated contemporary use of traps, and practices regarding animals that are considered inedible or too dangerous to hunt, including the warri, colored anteater, eleven banded armadillo, white-nosed coati, spider monkey, and jaguar.

(sample of 104 hunts). Hunting parties average two individuals for night-time and daytime hunts without dogs.

The total harvest of game from successful hunts (in kg) over the 13 month fieldwork period is lower in the directly observed GPS/HR sample, 190 kg (n = 16 prey items), than in the Notes sample 560 kg (n = 37 prey items) or in the HA sample 1,001 kg (n = 68 prey items). A similar but more accentuated pattern is observed for the harvests in kcal (Fig. S2), where unsuccessful hunts (kcal = 0) lower the median hunting return values in every sample (see SM Sect. 3 for further details on divergences in harvests obtained by different methods).

Where known, the average hunting trip duration is 4.9 ± 2.1 h. Considering successful hunts by prey type (Fig. 4), the one warri hunt observed is the longest at 7.8 h. In descending order of average duration are hunts for armadillo (5.9 h; sample of 25), gibnut (4.9 h; sample of 14), peccary (4.5 h; sample of 33), and agouti (4.3 h; sample of 7). Hunts for deer are the shortest (3.1 h; sample of 5).

The probability of capture success on a hunt is double with dogs (0.6; sample of 105 trips) than without them (0.3; sample of 31 trips). Likewise, the total average harvest per

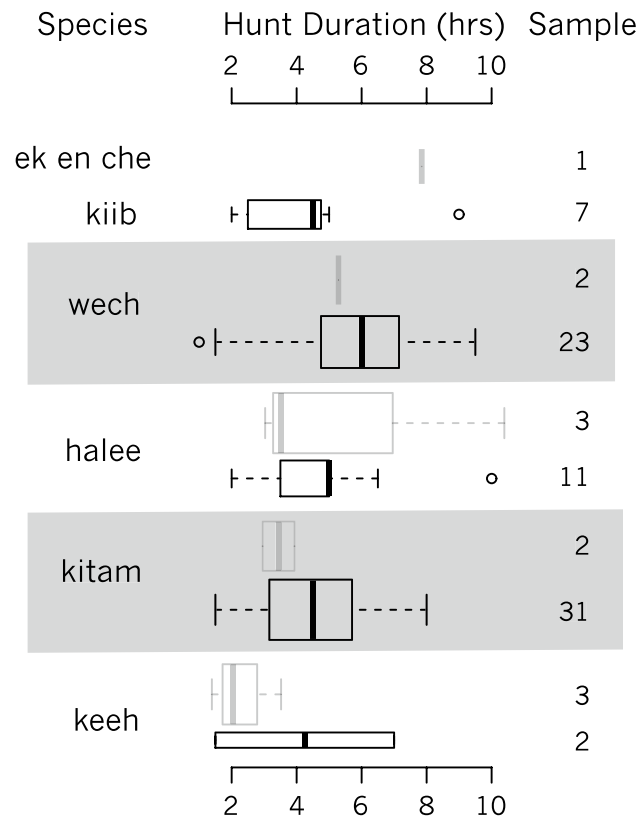


Fig. 4 Hunting trip duration by prey type captured. Hunts without dogs are depicted by gray-scale whiskered boxplots, those with dogs by black; our ek en che and kiib sample is either one or the other. We here omit 28 successful hunts for which duration is not available. We also omit here two atypical cases resulting in the capture of a wild pigeon and an iguana (see Notes in Table S1)

trip with dogs is higher (8.7 kg; sample of 143 trips) than without them (7.6 kg; sample of 42 trips). The latter ratio of harvest means increases if we consider the kilocalories harvested with dogs (18,055) and without them (10,642) (Fig. 5). A t-test for difference of means between the kilocalories acquired with and without dogs is significant at the $p = 0.03$ level ($t = 2.1$, $df = 79.3$, 95 PCI: 567, 14,259).

The presence of dogs is associated with captures of the most frequently hunted species: peccary, armadillo, and gibnut (Table 4). We observed single prey captures on 79 trips, double prey captures on 17 trips, a triple gibnut capture on a single night trip without dogs, and a quintuple armadillo-family capture on a single day trip with dogs. All double prey captures per trip were dog-assisted and all but one were in the daytime; they entailed six hunts that produced only peccary, three capturing only armadillo, and one each for deer, gibnut, and agouti. The remaining five hunts produced captures in these combinations: gibnut-agouti, deer-armadillo, agouti-armadillo, armadillo-gibnut, and peccary-armadillo.

The full list of local Santa Cruz fauna (Table S2) constitutes about three times the number of prey types that hunters elect to pursue, with or without their dogs. Animals such as the collared anteater are reported by elders to have been eaten in the past; others like the spider monkey or the eleven-banded armadillo are not considered by most villagers as fit for human consumption (see also SM Sect. 7).

Successful hunters sell meat for \$2 BZD/lb in Santa Cruz once they have satisfied their own household's needs. Interviewees (70%, n = 53) report buying bush meat from 17 village households. Households with active hunters, followed by occasional hunters are among those from which survey respondents buy meat. The regularity with which reporting households (54%, n = 41) buy meat is 2.3 ± 3.9 times/month. Sale usually entails cuts of peccary, armadillo, or gibnut, and less frequently deer (Table 4). Only a few villagers hunt in order to sell game outside the village.

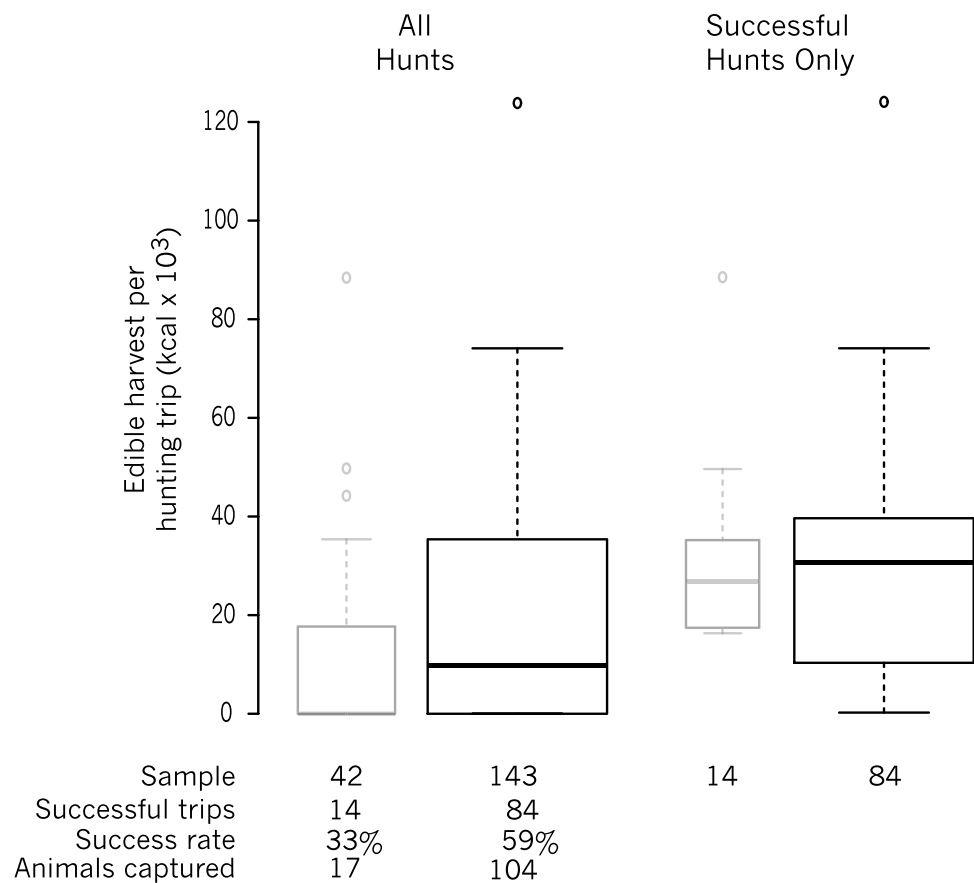
Discussion

Cultural Ecology of domestic dogs

Comparative Demography

Santa Cruz's human:dog ratio (2.9:1) is within the range (1.7:1 to 4.6:1) reported for three Maya communities in rural Yucatan (Ortega-Pacheco et al. 2007) but is below the 3.7:1 and 5.7:1 reported for two villages with similar human population sizes on Mexico's Pacific Coast (Ruiz-Izaguirre et al. 2014). Habitat type and/or the specific use of dogs might account for the differences. For example, in the Isoso indigenous territory of Bolivia Fiorello et al. (2006) estimate

Fig. 5 Whiskered boxplots of total edible harvest recorded per trip, without (gray) and with (black) dogs, for all hunts (kcal ≥ 0) and for successful hunts (kcal > 0). The harvest median (bold bar) is higher when dogs are used for hunting. To convert harvest units from kilograms to kilocalories, we followed the procedure presented by Hill and Hawkes (1983)



a regional human:dog ratio of 1.5:1. Dogs are present in nearly all households and are considered necessary for hunting terrestrial species. In the urban and sub-humid savannah

climate of Bamako, Mali, where dogs are kept primarily as guards, the human:dog ratio is 121:1 (Mauti et al. 2017). Our intra-village data is consistent with this trend. On a gradient

Table 4 Prey captures recorded during fieldwork in Santa Cruz

Species ¹	N	Kg ³ (mean \pm sd)	Hunted without/with dogs	Mopan Maya	Kekchi ⁴	English	Spanish
<i>Tayassu pecari</i> ^{VU, 2}	1	45.4	1/0	Ek en che	Chacow	White-lipped peccary (warri)	Coche de monte
<i>Odocoileus virginianus</i> ^{LC}	8	37.7 \pm 13.9	4/4	Keeh	Que ej	White-tailed deer	Venado cola blanca
<i>Mazama americana</i> ^{DD}	1	34	1/0	Yuk	Yu uq	Red brocket deer	Cabro de monte
<i>Pecari tajacu</i> ^{LC}	48	19.3 \pm 5.3	2/46	Kitam	A ak	Collared peccary	Saino
<i>Cuniculus paca</i> ^{LC}	21	11.1 \pm 5.3	7/14	Halee	Jalaw	Gibnut (paca)	Tepezcuintle
<i>Dasyopus novemcinctus</i> ^{LC}	32	5.7 \pm 2.3	2/30	Wech	Aj huech	Nine-banded armadillo	Armadillo de nueve bandas
<i>Nasua narica</i> ^{LC}	1	3	0/1	Chiic	Siis	White-nosed coati (quash)	Pizote / Tejón
<i>Dasyprocta punctata</i> ^{LC}	7	2.9 \pm 1.2	0/7	Kiib	Akam	Central American agouti	Guatusa
<i>Iguana iguana</i> ^{LC}	1	2.7	0/1	Garuba	Igwan	Green iguana	Iguana
Bird (not identified)	1	0.5	0/1			Wild pigeon	
Total	121		17/104				

¹Red List conservation status, by species (IUCN 2020): Data Deficient (DD), Least Concern (LC), and Vulnerable (VU)

²This hunt took place in Golden Stream, about 40 km northeast of Santa Cruz

³Most of our prey weights (n=85) come from hunters' estimates or actual measurements; the remainder (n=36) were taken from averages reported in the literature (see Methods section)

⁴Kekchi names provided by A. Maas, after identifying the species in the Rainforest Publications (2009) field guide

from active hunter to non-hunter households (Table 2) we observe a gradual decrease in the household:dog ratio and an increase in the guard:hunter dog ratio. The high number of canids associated with active hunter households is consistent with the pattern for indigenous hunters in Nicaragua (Koster and Noss 2014).

Our informant estimates of adult dogs' lifespans match observations from Asia (Nobayashi 2006) and Africa (Lupo 2011). Reports of high mortality rates of hunting dogs due to accidents or encounters with their prey or non-prey predators (Ikeya 1994; Jones 1970; White 1972) also reflect our results. Santa Cruz villagers associate the high mortality of pups (80%) with stomach infections, matching two of the main causes of death (diarrhea or worms) for puppies (73%) reported by Bolivian hunters (Fiorello et al. 2006). Low first-year survival rates in Santa Cruz also could be the result of malnutrition in lactating females, for whom the standard Santa Cruz tortilla diet would cover only 25% of their daily energetic requirement (DER) if they were feeding two puppies (Thatcher et al. 2010). Unfortunately, we do not know if Santa Cruz households augment the diet of lactating females. Low survival rates for pups are also observed in Bamako city, Mali, where 73% of pups die during their first year (Mauti et al. 2017) and in the coastal villages of Michoacan, Mexico, where many pups do not survive more than a few weeks (Ruiz-Izaguirre et al. 2014).

Functions and Training

The use of dogs to guard crops and households and as hunting aids is also found in Maya communities of the Yucatan Peninsula and Mexico's Pacific Coast, where rural dogs provide security, companionship, hunting and herding services according to Ortega-Pacheco et al. (2007). The same functions have been reported in forest-mangrove environments, Los Petenes, Campeche (Plata et al. 2019), and in Nahua and Mestizo coastal communities (Ruiz-Izaguirre et al. 2015). The use of dogs in hunting is associated with semi-agricultural landscapes in Nicaraguan Mayangna and Miskito communities (Koster 2008b); dogs are identified with crop-raiding control in the Brazilian Médio-Jurúa region (Abrahams et al. 2018). We have no evidence of intentional breeding for favored hunter or guard dog traits, similar to Koster and Noss's (2014) observations among the Mayangna and Miskito of lowland Nicaragua.

Dog training in Santa Cruz is passive in the sense that it consists of encouraging natural variation in their inclinations. Likewise, Plata et al. (2019) observe that hunting dogs in Los Petenes develop their skills through practice, prompted by the hunters and the guidance of more experienced dogs. The intra-pack specialization of Santa Cruz dogs into *chabe* and *alca* roles are analogous to the maestro (leader) and secretario (apprentice) dogs from Los Petenes

(Plata et al. 2019). Interviewing in Spanish and English, we may have missed deeper appreciation of divergent canine hunting roles. Plata and collaborators (2019) notice that mongrel dogs are preferred over pure breeds, as they are known to be sturdy in the *batida*, a Spanish term for group hunts in the Yucatán.

Maintenance

Most dogs in Santa Cruz and other locations in the Neotropics are home born or received as gifts (Fiorello et al. 2006; Ortega-Pacheco et al. 2007). Purchase in Santa Cruz occurs mainly among active and occasional hunter households (Table 2) as an investment in maintaining a stock of hunting dogs. Koster and Noss (2014) report that some residents buy multipurpose dogs in nearby Mestizo communities where the cost of a puppy is equivalent to 5 kg of meat. In Santa Cruz, the cost of a puppy or an adult dog is equivalent to 1 kg or 4 kg of meat, respectively. This difference in costs could depend on the distance to the communities where dogs are bought, or the price of meat within or outside hunters' villages.

Given that Santa Cruz hunting dogs typically have a shorter lifespan than guard dogs and that some hunters castrate their hunting dogs, it is possible that within the village there is selection against hunting motivation and ability. If so, buying hunting dogs from outside the village would mitigate the negative implications of village dogs reduced genetic fitness. Neutering dogs has the further advantage that it lowers their energy requirements, effectively elevating the five-tortilla diet from 44 to 55% of a 12 kg, moderately working dog's DER (Thatcher et al. 2010). The five-tortilla ration represents 129 g or 400 kcal/day (USDA 2017), 74% of the DER of guard dogs, which are relatively inactive and prone to obesity. Although useful for estimating owners' direct investment in dogs, these figures do not include the daily energy intake obtained from successful hunts, sporadic predation on small animals, household discards, and scavenging and thieving (Losey et al. 2014; Redfield and Villa Rojas 1962:231). Ortega-Pacheco et al. (2007) report dogs that are fed once a day or every other day search for food at dumps or in other households.

The Maya are reported to have been feeding their dogs with corn since the Preclassic (Tykot et al. 1996). According to Benedict and Steggerda (1936) (cited in White et al. 2001:101) in the early twentieth century dogs kept by Maya consumed an average of six to eight tortillas per day. This would represent 480 to 640 kcal/day, comparable to the average feeding regime of active hunting dogs in we found in Santa Cruz (Table 2), or to Ruiz-Izaguirre et al.'s (2015) estimate that 8.8 50 g tortillas meet the daily protein requirement (22.9 g) of an 18 kg adult dog.

With vaccines often free of charge, Santa Cruz households without active hunters invest little in medicine. Most owned dogs in the Yucatán are not vaccinated against anything other than rabies (Ortega-Pacheco et al. 2007).

Dogs and Tropical Conservation

The presence of village dogs near protected areas or primary forests has been associated with potential loss of biodiversity, particularly if canids are free-ranging (Ruiz-Izaguirre et al. 2015). Santa Cruz dogs appear not to enter primary forest areas on their own, perhaps to avoid predation by larger carnivores. And, because hunting in Santa Cruz is oriented opportunistically to control crop-raiding by medium sized herbivores, it may represent less of a threat to primary forest wildlife. An analysis of prey reproductive rates by Koster and Noss (2014) indicates that the species most frequently hunted in Santa Cruz—peccary, armadillo, and gibbon—can sustain relatively high harvests. Koster (2008a) finds that dogs are relatively ineffective in pursuits of species that are most vulnerable to overhunting. Constantino (2019) compared the assemblages of species hunted with and without dogs in the Brazilian Amazonia, concluding that there is no conservation-related reason to prohibit subsistence hunting with mixed-breed dogs.

Although trade in bushmeat with individuals not resident in Santa Cruz seldom occurs, the recent opening of a paved highway through the village could lead to increased frequency of this practice. If so, monitoring of wildlife populations matched to studies of strategies for hunting them sustainably may well become important (Ripple et al. 2016). Camera-trapping (Abrahams et al. 2018; Mella-Méndez et al. 2019) and radio- or GPS-tracking of dog movements (Ruiz-Izaguirre et al. 2015) combined with behavioral observations will be useful if these efforts are undertaken.

Subsistence Hunting

The disparities between our observed and subject-reported frequencies and success of hunting trips could have different causes, historical changes in settlement and economy among them (SM Sect. 7). For example, Thompson (1930) lists eight bird species that were hunted by Maya in Toledo District almost a century ago, but interest in hunting birds appears to have declined.

Hunting provides a modest amount of wild game to the diet (4.1 kg or 7076.9 kcal per capita annually if shared out equally among all villagers). Because active hunters hunt on average about every two weeks, they are providing their household wild meat about once a month. Similar to the

findings of other researchers for tropical forest environments (Alves et al. 2009; Bulmer 1968; Jones 1970; Koster 2009; Lupo 2011), hunting dogs in Santa Cruz are most helpful in the pursuit of prey that can be cornered. Except for great curassow (*Crax rubra*) and crested guan (*Penelope purpurascens*), the species hunted in Santa Cruz overlap with those reported by Doherty (2005): paca, warri, peccary, red brocket deer, white-tailed deer, and nine-banded armadillo.

Night hunting with dogs occurs among societies from regions as diverse as the eastern New Guinea highlands (Dwyer 1974), the Central Kalahari (Ikeya 1994), and Northeastern Brazil (Alves et al. 2009) to take advantage of canids' superior vision and olfactory capacities. Although undertaken without canines, the night hunting tactics we observe in Santa Cruz for deer or gibbon (see Results or SM Sects. 6–7, respectively) are similar to stalking, night-light hunting, and opportunistic tactics described by Leon and Montiel (2008). Santa Cruz hunters and their dogs behave as do batida hunters when hunting peccaries, however the largest party size in Santa Cruz is less than half the average number of humans participating in true batidas. Redfield and Villa Rojas (1962:366) argue that the introduction of guns and lamps to the Yucatán Peninsula made hunting more efficient. Similarly, Hames (1979) compares effective capture distance and hunting inputs and outputs to show the superiority of shotguns over indigenous weapons in Venezuelan Amazonia. For daytime hunts, our qualitative observations suggest that the introduction and use of firearms could have reduced pursuit time and improved safety when hunting with dogs, as prey could be killed more quickly and at a greater distance.

Although the presence of dogs does not always increase the probability of success or total harvest (Lupo 2017), we find a positive relationship (Fig. 5) comparable to that of male hunters in similar Neotropical habitats (Koster 2008a; Constantino 2019) or women hunters in Asian tropical forests (Griffin and Griffin 2000). In some cases, the presence of dogs extends the duration of hunting trips (see deer, gibbon, and armadillo, Fig. 4). Armadillo hunts tend to be longer due to extended searches in areas of bush distant from the village and agricultural fields. Gibbon hunts without dogs involve ambushes that can be short once game appears. Dogs are known to be inefficient in cornering large ungulates such as deer (Lupo 2017; Koster and Noss 2014), although evidence from batidas in Yucatán indicates that average party sizes of 20 hunters and four dogs take about eight hours to track and kill deer with a 75% success rate (León and Montiel 2008; Rodríguez et al. 2012). As described by Teit (1900:244–245) among Nlaka'pamux hunters in British Columbia, dogs in Santa Cruz occasionally are successful in hunting deer if they can force them into rivers where the hunters can drown them.

Evolutionary perspectives

Milpa protecting dogs

As has been observed in other Maya villages in Belize (Doherty 2005), contemporary hunting in Santa Cruz is oriented in part to protect maize crops from peccaries, gibnuts, coatis, raccoons, and other medium-size herbivores. Crops are especially vulnerable in the early and late stages of growth. Deer visit milpa fields to eat sprouts and young plants during May–June; peccaries eat green or mature corn from late July to early October. A group of peccaries ($n=3-9$) can eat up to 75 m² of maturing or mature corn in a single night-time visit. If a farm is left unprotected peccaries could consume a tarea (522.58 m²) of planted corn in a week according to a farmer who lost almost half of his plantation in 2011. An observational study sufficient to quantify the field protection benefit of dogs is not feasible through standard ethnography. Nonetheless, we can make indirect estimates. The average yield of corn in Santa Cruz is 1,830 kg/ha in dry grain (Cortez 2016); thus, the 75 m² single night consumption of peccaries represents 13.7 kg, or enough dry corn to feed a dog on a five-tortilla diet for 106 days. By chance, 106 days is almost the entire growing season of tropical lowland, dry harvest maize in Santa Cruz milpas (Cortez 2016). Even if a dog prevents only one nights' depredation by peccaries, it will have paid for its rations over the whole of the growing season, a benefit that could have encouraged farmers to keep dogs even if the pests they deter are not killed. Over a year, the cost to a Santa Cruz family of provisioning three to five dogs would be approximately 10% (7.7% to 12.9%, respectively) of their corn crop.

The association of dogs with agriculture and village life in Mesoamerica has a long history and extends well beyond the material considerations we have highlighted. Valadez and Blanco (2005) document the close relationship between the reproductive cycle of the dog and the milpa agricultural cycle in pre-Hispanic Mexico; rural canine estrus cycles parallel the preparation of agricultural fields for cultivation (mid-February to early-April) and the harvest of green corn (mid-August to early-October). They argue that this facilitated the incorporation of canids into ritual spheres, linking them to fertility, rain and thunder, and spiritual domains (see SM “Sect. 8: Dogs in Maya Myth and Folklore”). Despite differences in rainfall patterns, milpa field preparation and harvest times in Santa Cruz (Cortez 2016) correspond with those observed in Mexico. De Landa (1938) notes the use of dogs to hunt birds and flush deer, probably into traps, in pre-Columbian times. Based on current ethnographic evidence and taphonomic studies, Ley-Lara and Götz (2016) conclude that canids in pre-Hispanic Yucatán could have acted as companions, as hunting aids, as village and field guards, and to dispose of food debris.

Dogs and the Origins of agriculture

The starch digestion genes present in domestic dogs were likely selected as a genetic adaptation to commensal living with humans engaged in cultivation (Axelsson et al. 2013). Larson et al. (2012) use the example of Coxcatlan Cave in Mexico where dog remains from 5,200 BP overlap the appearance of agricultural communities to argue that as agricultural societies developed the appearance of dogs south of the original wolf distribution in the Old and New Worlds coincided with the development of agriculture. In her archaeological analysis of 960 AD faunal assemblages in Cerro Brujo, Panama, Linares (1976) observed that about half of the animals in her sample showed evidence of having consumed cultivated crops. Linares developed the idea of “garden hunting,” as cleared field and garden plots had the additional benefit that they attracted easily harvested game. Field guarding by dogs could have enhanced the advantages of garden hunting by forestalling excessive depredation of crop production by herbivores while also elevating the odds of their capture.

In non-hunter households dogs are used mostly as guards, a use that may have been recognized by humans early in the domestication process and possibly before their use in hunting (Driscoll and Macdonald 2010; Manwell and Baker 1984). Nevertheless, dogs may have played a key role not only in hunting but in the successful expansion of agriculture, with their predatory abilities, territorial proclivities, and altruistic and social behaviors inherited from wolves (Driscoll and Macdonald 2010; Jouventin et al. 2016). In the late Pleistocene, the residues from field processing of game by central place foragers may have provided an early context for dogs to affiliate with human hunting activities; central place aggregation may have drawn canines to camp life, where they scavenged decaying waste; and field crop and stored food protection and the benefits of hunting aid in turn enhanced the success of human subsistence pursuits. Late Pleistocene-Holocene hunters assisted by dogs would have then experienced increased encounters with prey and higher success rates, particularly in tropical environments where canids can effectively corner game. Archaeological evidence of human–dog interactions around migratory hunter-gatherer camps or in early agricultural settlements can be found in animal bones remains with marks of mastication by dogs (Ley-Lara et al. 2015).

Concluding Summary

- Santa Cruz dogs guard households and fields and they aid in hunting success. Guard dogs do not hunt, but hunting dogs act also as guards. Hunting dogs have significantly shorter lifespans due to the hazards of forest pursuit. The

association of dogs and agriculture has a long history in Mesoamerica.

- A household's use of dogs affects its investment in them. On a gradient from hunting to non-hunting households there is a gradual decrease in the number of dogs kept, litters born, and food and medical care provided.
- Dogs in hunting groups tend toward either acting as *chabe* (guide) or *alca* (runner). Further investigation of intra-pack roles may be fruitful.
- Hunts that include dogs appear to have a higher probability of success and result in higher caloric harvests than those without dogs. Dogs in tropical lowland Santa Cruz are not used in night-time hunting, they are protected from hunting dangerous prey, and they generally are not effective in hunting swift cursorial animals like deer in this environment. Training relies on modest efforts to encourage behavioral inclinations that otherwise emerge spontaneously.
- Except for the warri, the herbivores hunted in Santa Cruz have demographic properties that allow to sustain even relatively high rates of harvesting, reducing the conservation concerns.
- The balance between the costs of milpa- and household-protecting dogs and the subsistence benefits they provide is favorable for their maintenance. We hypothesize that dogs may have had a role in some instances of agricultural origins and expansion, by helping to obtain meat via garden hunting while also protecting growing crops in the field and harvested stores at the homestead.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10745-021-00261-w>.

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Declarations

Conflict of Interest The authors declare that they have no conflict of interest.

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