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Identification of kill sites from GPS clusters for jaguars (*Panthera onca*) in the southern Pantanal, Brazil

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Abstract

Context. Understanding predator–prey relationships is important for making informed management decisions. Knowledge of jaguar (*Panthera onca*) predation on livestock and native prey is imperative for future conservation of jaguars in Central and South America.

Aim. As part of an investigation to determine predation patterns of jaguars in the southern Pantanal, Brazil, we examined spatial, temporal and habitat variables, which are useful in categorising location clusters as kill sites and non-kill sites.

Methods. Using GPS-collars on 10 jaguars we obtained a total of 11 784 locations, from which 877 clusters were identified, visited and examined for prey remains. Of the 877 clusters, 421 were associated with a kill and 456 clusters were not associated with a kill. We used univariate and multivariate models to examine the influence of spatial (distance to nearest: water, dense cover, road; dispersion of points), temporal (season, time, number of nights, duration) and habitat (percentage of seven habitat classes, dominant habitat class) variables on categorising clusters as kill or non-kill sites.

Key results. We found the time a jaguar spent at a cluster (duration), the dispersion of points around the centre of the cluster (dispersion) and the number of nights spent at the cluster were all reliable predictors of whether a cluster was a kill or non-kill site. The best model predicting the likelihood a cluster was a jaguar kill site was a combination of duration and dispersion. Habitat variables were not important in discriminating kills from non-kill sites.

Conclusion. We identified factors useful for discriminating between kills and non-kill sites for jaguars. We found that as a jaguar spent more time at a cluster and as the dispersion of points around the centre of the cluster increased, the higher likelihood the cluster was a jaguar kill. Similarly, as the number of nights spent at the cluster increased, the greater the probability the cluster was a kill.

Implications. Our results will increase the efficiency of field investigations of location clusters in determining predation patterns of jaguars in Central and South America. Being able to prioritise which location clusters should be investigated will assist researchers with limited time and resources.

Additional keywords: cluster analysis, global positioning systems (GPS) radio-collars, kill sites, non-kill sites, predation.

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Introduction

The interaction between predators and their prey has long been of interest to ecologists and is one of the fundamental tenets of ecology (Errington 1967; Lima and Dill 1990; Barbosa and Castellanos 2005). Knowledge of predator-prey relationships is paramount to making informed management decisions, but acquiring detailed observations on predation is extremely difficult to obtain for large secretive carnivores. Snow-tracking of large carnivores from the air and ground can yield prey remains (e.g. Mech 1966; Peterson 1977; Atwood *et al.* 2009), but determination of kill rates of secretive carnivores typically requires capture, radio-collaring and intensive radio-tracking of individual animals for more reliable and efficient relocation (e.g. Smith *et al.* 2004). While the use of very high frequency (VHF) radio-collars has allowed for the determination of predation rates for many carnivores dwelling in northern latitudes, particularly cougars (*Puma concolor*; e.g. Murphy 1998; Cooley *et al.* 2008; Ruth 2004) and wolves (*Canis lupus*; e.g. Kunkel *et al.* 1999; Jędrzejewski *et al.* 2002; Smith *et al.* 2004), the absence of snow cover and dense vegetation in southern latitudes make such investigations almost impossible. With the advent of global positioning system (GPS) radio-collars, our ability to acquire data on predation patterns and kill rates of large carnivores has increased substantially (e.g. Webb *et al.* 2008; Knopff *et al.* 2009; Merrill *et al.* 2010; Tambling *et al.* 2010; Martins *et al.* 2011; Pitman *et al.* 2012;

Elbroch *et al*. 2013; Miller *et al*. 2013). During early studies using GPS collars, Anderson and Lindzey (2003) demonstrated that GPS locations collected within a particular time-frame and distance from each other could be used to evaluate if clusters of locations were most likely associated with a kill. Since then, multiple studies on large carnivores have used GPS collar locations to determine which clusters are potential kill sites (e.g. Sand *et al*. 2005; Webb *et al*. 2008; Knopff *et al*. 2009; Ruth *et al*. 2010; Tambling *et al*. 2010; Martins *et al*. 2011; Pitman *et al*. 2012; Krofel *et al*. 2013; Miller *et al*. 2013). Interestingly, as technology has advanced and the use of GPS collars has increased, the volume of locational data has also increased, creating a situation that is both beneficial and deleterious. The large amount of data allows researchers to access locations at both spatially and temporally fine scales while at the same time generating too many clusters that can be realistically investigated in the field to determine if they are kill sites or sites associated with other behaviours not related to predation (e.g. Webb *et al*. 2008; Knopff *et al*. 2009; Ruth *et al*. 2010; Krofel *et al*. 2013).

As jaguars (*Panthera onca*) are the apex predator in Central and South America, understanding the role of jaguar predation in the southern hemisphere is important for their long-term conservation and population persistence. Particularly, knowledge of predation on domestic livestock will be needed to alleviate or manage conflicts between jaguars and local ranchers (Azevedo and Murray 2007; Cavalcanti *et al*. 2010). However, the combination of dense vegetative cover, low animal density, secretive behaviour, little road access and lack of snow cover make the use of conventional VHF collars particularly difficult in determining predation patterns of jaguars. The use of GPS collars created the possibility of obtaining information in the southern Pantanal of Brazil on jaguar kill rates, composition of prey killed and handling times of both native prey and domestic cattle (Cavalcanti and Gese 2010). In addition, the use of GPS collars provided information on space use and social interactions (Cavalcanti and Gese 2009). Almost half of the GPS collar location clusters were not associated with predation events, but rather with other behavioural activities (e.g. bed sites, dens, social interactions; Cavalcanti and Gese 2010). Knowledge of (or an ability to differentiate among) GPS location clusters to identify 'kill sites' and 'non-kill sites' for jaguars would increase efficiency in determining which cluster to search, particularly when logistical constraints reduce the number of clusters that can be visited and examined for prey remains (cf. Webb *et al*. 2008; Knopff *et al*. 2009).

In this paper, we differentiate between jaguar kill sites and non-kill sites using temporal, spatial and habitat characteristics of GPS location clusters in the southern Pantanal of Brazil, to improve the probability of determining whether a cluster was associated with a jaguar kill before field investigation and provide recommendations for selecting which clusters to visit to optimise site visitation. We hypothesised that clusters identified as kill sites would have a greater number of locations and that jaguars would remain at them longer than clusters identified as non-kill sites, that kill sites would be in certain habitats (mainly habitats containing dense cover for ambushing prey, or habitats preferred by their main prey) and that kill sites would be initiated at different times of the day than non-kill sites. We did not attempt to associate cluster duration with prey size due to small sample sizes of large, medium and small prey-size classes (Cavalcanti and Gese 2010). Through these efforts, we hope our research will assist future wildlife biologists to determine which GPS location clusters have the highest potential to be jaguar kill sites and thereby improve field assessment efficiency.

Materials and methods

Study area

The study area consisted of a 460 km^2 privately owned ranch located in the southern Pantanal, Brazil. The Pantanal is a 140 000 km^2 floodplain in west-central Brazil that experienced a dry and wet season. The dry, cool season (April to September) received a mean monthly precipitation of 48 mm with temperatures reaching as low as 18°C in June and July. The hot, wet season (October to March) received a mean monthly precipitation of 145 mm and temperatures reached 42°C in October (Cavalcanti and Gese 2010). The low topographical relief (89–120 m above sea level) resulted in a substantial reduction of accessible habitat during the wet season when much of the area was inundated with water.

The vegetation was a mosaic with influences from several biomes such as cerrado in central Brazil, the Paraguayan Chaco, and the Amazon Forest (Prance and Schaller 1982). We delineated seven habitats on the study area, according to the degree of canopy closure, vegetation density and species composition. The seven habitats were: (1) Brushland (21% of the area) was characterised by different shrubs (e.g. *Vernonia scabra*, *Annona dioica*, *Bauhinia* spp., *Psidium guineense*, *Cordia insignis*) and small trees (e.g. *Erythroxylum suberosum*, *Banara argutta*, *Alchornea discolor*) varying in height from 2–4 m with dense cover; (2) Dense riparian forest (21%) consisted of areas remaining wet for longer periods into the dry season. This habitat was characterised by thick heterogeneous clumps of shrubs, herbaceous vegetation and gallery forests along river corridors. (3) Dense upland forest (4%) was a combination of secondary forest and open forest patches, and was characterised by trees with a high (6–20 m) thick canopy. The principal species were deciduous, semideciduous and palm trees (e.g. *Ceiba samauma*, *Genipa americana*, *Guazuma ulmifolia*, *Sterculia apetala*). The understory of dense upland forests varied from open to semiclosed to almost completely closed; (4) Herbaceous field (6%) consisted of tall grassland species with wide leaves and soft stems (e.g. *Echinodorus macrophyllus*, *Heliconia* spp., *Cyperus giganteus*, *Ipomoea carnea fistulosa*), varying in height from 50 to 200 cm, according to the season. This habitat was usually submerged during the wet season; (5) Open field (22%) was the most open habitat, and included bare soil and various short grassland species, both native (e.g. *Andropogon bicornis*, *Leersia hexandra*, *Paspalum almum*) and introduced (e.g. *Brachiaria humidicula*) species, 50–100 cm in height; (6) Savannah (20%) was similar to open field, but was interspersed with different species of deciduous, semideciduous or palm trees (e.g. *Tabebuia* spp., *Ficus* spp., *Curatella americana*) and included small tree islands on slightly elevated ground that remained dry during the wet season; (7) Wetland (6%) contained areas of open water and vegetation that was wet throughout the year, and included *Eichhornia* spp., *Typha domingensis*, *Lymnocharis flava*, and *Oxycaryum cubense.*

The ranch supported ~6000 cattle (*Bos* spp.) and native wildlife species including white-lipped peccary (*Tayassu pecari*), collared peccary (*Pecari tajacu*), caiman (*Caiman crocodilus yacare*), marsh deer (*Blastocerus dichotomus*), brocket deer (*Mazama americana* and *M. gouazoubira*), feral hog (*Sus scrofa*), capybara (*Hydrochoerus hydrochaeris*) and numerous small mammals, birds and reptiles (Cavalcanti and Gese 2010). Other large mammalian predators in the area included cougar (*Puma concolor*) and maned wolf (*Chrysocyon brachyurus*). During the dry season, cattle were dispersed throughout the study area, but during the wet season, cattle were herded into drier areas but remained dispersed over large pastures.

Capture and radio-collaring

To capture jaguars, we searched for recent jaguar tracks on the study area from horseback or from a vehicle in the early morning hours. After finding recent tracks, we released trained hounds in an attempt to tree the jaguar (Hornocker 1970; Crawshaw and Quigley 1991; Murphy 1998; Ruth 2004). We then immobilised the treed jaguar with tiletamine hydrochloride and zolazepam hydrochloride (Telazol, Fort Dodge Animal Health, Fort Dodge, IA), or a combination of Telazol and ketamine hydrochloride (Fort Dodge Animal Health, Fort Dodge, IA) administered with a dart pistol or rifle (Cavalcanti and Gese 2009, 2010). Upon darting, we removed the hounds from the immediate area. We measured each jaguar for body condition, sex, age and weight, fitted them with a GPS radio-collar (Televilt International, Lindesberg, Sweden) and released them at the site of capture. Age was estimated from the presence of milk or permanent teeth, amount of wear and colour of the teeth (Ashman *et al*. 1983). We placed each jaguar into one of three age classes: adult (>24 months old), subadult (11–24 month old) and kitten (<11 months old); no kittens were radio-collared. Capture and handling protocols were conducted under approval by the Institutional Animal Care and Use Committee (IACUC) at the National Wildlife Research Center (QA-1194) and Utah State University (permit #1202).

Determination and investigation of GPS location clusters

We obtained locations from the GPS radio-collars with a high degree of accuracy and precision (ground tests with reference GPS radio-collars showed error was <10 m (Cavalcanti and Gese 2010). We initially programmed the GPS radio-collars to obtain locations every 2 h between 1800 and 0600 (seven locations per night) to capture their activity during the suspected period of highest activity (Schaller and Crawshaw 1980; Beier *et al*. 1995; Harmsen *et al*. 2009). After 2002, we programmed the GPS radio-collars to collect locations every 2 h throughout the entire day to capture jaguar activity equally across the 24-h period. We downloaded the GPS locations from each collar every 21–24 days via a radio link between the GPS radio-collar and a remote receiver (Cavalcanti and Gese 2009, 2010). We recovered the GPS radio-collars for battery replacement every 10–11 months by recapturing the jaguars using hounds.

Clusters of GPS radio-collar locations (hereafter referred to as 'clusters') were identified based on spatial and temporal constraints (Anderson and Lindzey 2003; Sand *et al*. 2005; Webb *et al*. 2008) and had two potential outcomes upon investigation in the field: either the cluster was a kill site or a non-kill site. The criterion used for identifying potential kill sites was when ≥2 consecutive locations (temporal constraint) were found <100 m from each other (spatial constraint), following the procedures described by Anderson and Lindzey (2003), Sand *et al*. (2005), and Webb *et al*. (2008). To locate and identify prey remains, clusters were searched within 1–21 days after cluster initiation out to a radius of 50 m from the approximate centre of the cluster. The ground search continued until the 100 m diameter area was thoroughly searched. Prey remains did not degrade within the time elapsed between cluster initiation and cluster search (Anderson and Lindzey 2003), as evidenced by prey remains being found at 36%, 34% and 38% of the clusters searched 1, 2 and 3 weeks after cluster initiation, respectively (Cavalcanti and Gese 2010). If prey remains (i.e. skeletal remains, hair, internal organs) were found at a searched cluster, the site was classed as a kill site and a GPS coordinate was obtained; where possible, species, sex, and age class of the remains were also recorded. If no remains were located within 100 m diameter from the centre of the cluster, the site was considered a non-kill site and the initial GPS cluster location was recorded as the cluster location. The time that the initial GPS cluster location occurred was recorded as the time of cluster initiation for both kill and non-kill sites. We recognise that smaller prey items may have gone undetected due to complete consumption or the remains being removed from the kill site by the jaguar or other scavengers. However, we did locate and identify several prey items <5 kg in size (Cavalcanti and Gese 2010).

We assumed all prey remains at kill sites were due to jaguar predation and not jaguars scavenging kills made by other species (Gonzalez and Piña 2002), or jaguars usurping other species kills (i.e. kleptoparasitism). As the apex predator in this system, jaguars experience little threat of kleptoparasitism from cougars, the next largest predator in the study area (Azevedo *et al*. 2010; de Oliveira and Pereira 2014). Jaguars are thought to rarely participate in scavenging and when scavenging occurs it is likely to be opportunistic (Gonzalez and Piña 2002; Platt *et al*. 2007; Castaneda *et al*. 2013). Even though cougars are susceptible to jaguar predation (de Oliveira and Pereira 2014) and potentially occupy the same dietary niche (Foster *et al*. 2013), few records of jaguar predation on cougars have been reported.

Model variables

We developed biologically relevant mixed-effects models examining four temporal, five spatial and eight habitat variables to determine which parameters would predict whether a cluster was a kill or non-kill site (Table 1). We did not examine jaguar sex or age even though those variables have been shown to have an influence on prey selection (Cavalcanti and Gese 2010) because GPS collar locations were not equally distributed among the sexes or age classes. We included the individual jaguar as a random variable to account for lack of independence among the GPS collar locations for each jaguar. The number of nights at a kill has been shown to be influential

Table 1. Temporal, spatial and habitat variables examined in generalised linear, mixed-effects models to assess if GPS collar clusters were associated with a jaguar kill in the southern Pantanal, Brazil

Habitat variables were the percentage within a 50-m radius circle around the cluster centre

Variable type	Variable name	Description
Temporal	Season	Dry or wet
	Period	Morning, day, evening, night
	Duration	Time (hours) a jaguar was associated with a cluster
	Nights	Number of nights a jaguar was associated with a cluster
Spatial	NR_water_d	Distance to nearest water (m) in dry season
	NR_water_w	Distance to nearest water (m) in wet season
	NDC	Distance to nearest dense cover (m)
	NR	Distance to nearest road (m)
	Dispersion	Mean distance from centroid for all cluster points (m)
Habitat	BR	% brushland
	DRF	% dense riparian forest
	DUF	% dense upland forest
	HF	% herbaceous field
	OF	% open field
	SV	% savannah
	WL	% wetland
	Dom_veg	Habitat class with the highest percentage

Table 2. The three univariate models, two additive models and the null model examining jaguar kill and non-kill sites in the southern Pantanal, Brazil

Rankings based on Bayesian Information Criteria (BIC), ΔBIC, degrees of freedom (d.f.) and weights. All models included a random variable of jaguar identification. Duration is the number of hours a jaguar spent at a cluster, dispersion is the mean number of metres from the geographic cluster centre to each GPS location and nights is the number of nights a jaguar spent at the cluster

Model	BIC	ΔBIC	d.f.	Weight	AUC
Duration + Dispersion	947.6	0.0	4	1	0.82
Duration	1005.0	57.4	3	<0.001	0.79
Nights + Dispersion	1015.3	67.6	4	<0.001	0.78
Dispersion	1079.3	131.6	3	<0.001	0.75
Nights	1110.6	163.0	3	<0.001	0.71
Null	1217.7	270.1	2	<0.001	–

Table 3. The three best performing univariate models and the null model examining jaguar kill and non-kill sites in the southern Pantanal, Brazil

Rankings based on Bayesian Information Criteria (BIC), ΔBIC, degrees of freedom (d.f.), and weights. All models included a random variable of jaguar identification. Duration is the number of hours spent at a cluster, dispersion is the mean number of metres from the geographic cluster centre to each GPS location, and nights is the number of nights a jaguars spends at the cluster

Model	BIC	ΔBIC	df	Weight
Duration	1005.0	0.0	3	1
Dispersion	1079.3	74.3	3	<0.001
Nights	1110.6	105.6	3	<0.001
Null	1217.7	212.7	2	<0.001

in predicting whether a cluster is associated with a cougar kill (Anderson and Lindzey 2003; Ruth *et al.* 2010), so we included the number of nights a jaguar was present at the kill as a variable. We speculated that the duration of time (rounded to whole hours, hereafter referred to as 'duration') spent at a cluster might differentiate between potential kill and non-kill sites and theorised that more time spent at a cluster might indicate a kill. We centralised and standardised duration at a cluster by subtracting the mean from each duration then dividing by the standard deviation across all duration times. Additional temporal variables examined were season (wet or dry) and period of the day when the time of the first cluster location occurred (morning: 4:00–9 : 59, day: 10:00–15 : 59, evening: 16:00–21 : 59, night: 22:00–3 : 59). The spatial information examined included distance (km) to the nearest water during the wet and dry seasons, distance (km) to the nearest dense cover, distance (km) to the nearest road and mean distance (km) from each point in the cluster to the geometric centre of the cluster (hereafter referred to as 'dispersion'). Habitat variables consisted of seven habitat classes generated from an unsupervised classification scheme of wet and dry season Landsat Thematic Mapper images (1:100 000; Cavalcanti 2008) in ERDAS Imagine 8.7 (Leica Geosystems Geospatial Imaging, Norcross, GA). We used the TM2 band (green), the TM3 band (red), the TM4 band (near-infrared) and the TM5 band (water absorption band) to generate nine habitat classes according to the degree of canopy closure, vegetation density and species composition (see Study Area for detailed habitat descriptions; Cavalcanti 2008). The original nine habitat classes were converted into seven classes (Table 1) because the bare soil and open water classes consisted of <3% of the area. Bare soil was incorporated into the open field class and open water was incorporated into the wetland class. We generated a 50-m radius buffer around each cluster centroid, which equalled the 100-m diameter of the search area, to determine the percentage of the seven habitat types and the dominant habitat type for each cluster in ArcGIS 10.2.2 (ESRI, Redlands, CA). The habitat class with the highest percentage presence in the 50-m radius buffer was considered the dominant habitat type. We did not examine elevation, slope, aspect or ruggedness because the Pantanal has little topographical relief and the study area was considered flat in topography (Cavalcanti and Gese 2010).

Model construction and analysis

We used univariate, generalised, linear mixed-effects models with the BOBYQA optimisation (Powell 2009) and 10 iterations (nAGQ = 10) to determine which variables were associated with the binary response of a cluster being a kill ($y = 1$) or a non-kill site ($y = 0$). Full models did not converge so we used a modified hierarchical model selection technique (Franklin *et al.* 2000; Hamer *et al.* 2006; McLaughlin *et al.* 2014) to generate biologically relevant models. We used Bayesian Information Criteria (BIC, Schwarz 1978) to rank the null and all univariate models (i.e. all variables in Table 1). Additive and interactive multivariate models (Table 2) were based on the variables associated with the best-ranked univariate models (Table 3). Model fit was assessed with area under the curve (AUC) based on the receiver-operator characteristic (ROC) curve

(Boyce *et al.* 2002). Models with AUC values of 0.5 are considered to have low performance while values of 1.0 are indicative of a perfect-model fit. All model development and analysis was conducted in the R statistical software (R Core Development Team 2014).

Results

We captured and radio-collared six adult male and four adult female jaguars from October 2001 to April 2004, monitored them for an average of 8.25 months (±6.98 s.d.; maximum = 24 months, minimum = 1.5 months) and obtained a total of 11 784 GPS locations. Of the 877 clusters visited, 421 were associated with a kill (i.e. prey remains were found at the cluster) and 456 were not associated with a kill (Cavalcanti and Gese 2010). Most of the kill sites were associated with a single prey species and only 14 sites were associated with multiple prey items. Individual jaguars differed in the proportion and prey species they killed, with some jaguars specialising on a few prey species and others exhibiting a generalist diet (Cavalcanti and Gese 2010). Of the 456 non-kill sites, 13 had evidence of scent marks, six were intraspecific interactions (two GPS radio-collared jaguars located in the same place at the same time), five were bed sites, and the remaining 432 clusters had no evidence of obvious behavioural activity or a predation event.

We examined all univariate models and ranked them according to BIC to determine which variables most influenced whether a cluster was a kill or a non-kill. Models performing better than the null were the univariate models of duration, dispersion and number of nights at the cluster. All other models had ΔBIC values ≥200 and weights ≤0.001 (Table 3). We generated multivariate models based on the three best-performing univariate models, although duration of time spent at a cluster and the number of nights present at a cluster were correlated ($r^2 = 0.77$) and therefore were not included in the same model. Comparison of the multivariate models, the three lowest ranked univariate models and the null model indicated that duration and dispersion best explained the likelihood a cluster was associated with a kill. The AUC for the additive model of duration and dispersion was 0.82, indicating the model fit the data well, while the AUC for the remaining models was ≤0.79 indicating a lower fit (Table 2).

As the amount of time a jaguar spent at the cluster increased, the proportion of clusters that were associated with kills increased (Fig. 1*a*). Generally, if a cluster was visited for ≥12 h by a jaguar, the cluster was more likely (>50% probability) to be associated with a kill, although 8% (35) of the non-kill sites were visited for >12 h. The longest duration of visitation by a jaguar was 106 h at a kill site of an adult cow, while the longest duration for a non-kill site was 98 h and may have represented a den site. Similarly to the duration of time at a cluster, as the number of nights a jaguar spent at a cluster increased, the more likely the cluster was associated with a kill (Fig. 1*b*); these two variables (duration and nights) were related. The maximum number of nights spent at a kill site was 5 nights, while the minimum number of nights was 0, indicating that some jaguars did not stay at the kill site for even 1 night. Finally, as the spatial dispersion of the cluster increased (i.e. the cluster

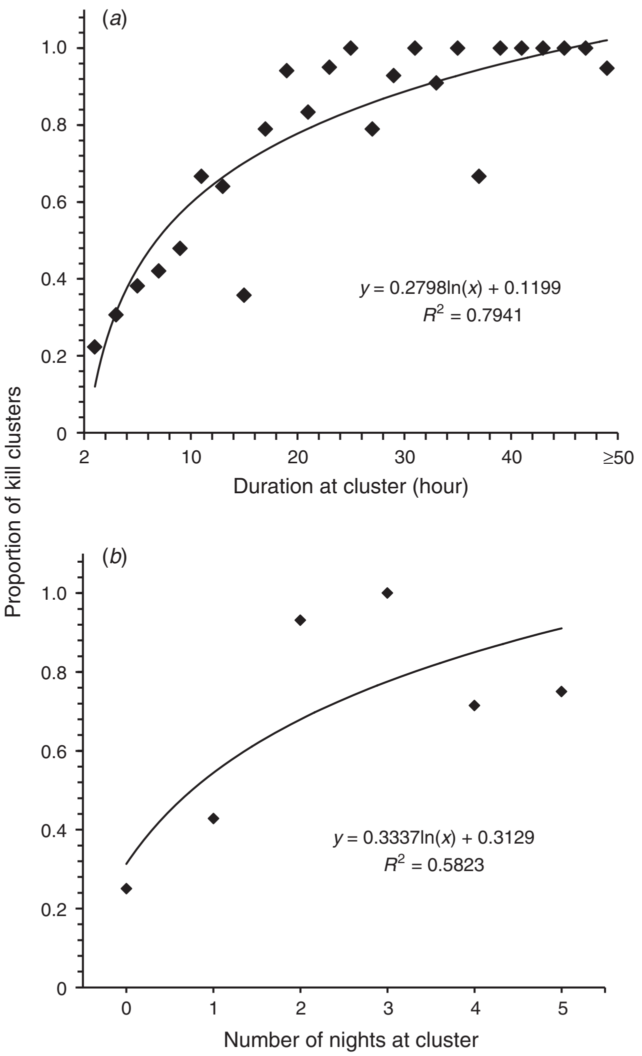

Fig. 1. Relationship between the proportion of clusters associated with a kill and (*a*) the duration of time spent (hours) at the cluster by a jaguar, and (*b*) the number of nights a jaguar spent at a cluster, southern Pantanal, Brazil.

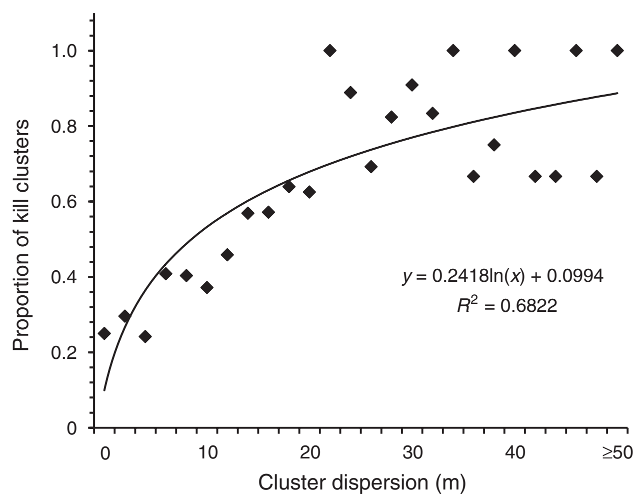

Fig. 2. Relationship between the proportions of clusters associated with a kill and the dispersion of the cluster (m) for jaguars in the southern Pantanal, Brazil.

increased in size), the proportion of clusters associated with a kill also increased (Fig. 2). The longer a jaguar remained at a cluster, either measured as the number of hours or the number of nights, and the larger the cluster size, the greater the proportion of clusters were associated with a kill. When duration and dispersion are examined together, clusters where a jaguar spent >50 h in duration and the dispersion of points was >60 m, the likelihood of that cluster being a jaguar kill approached 80–100% (Fig. 3). The increasing dispersion around the kill site seems counter-intuitive, but we emphasise this measure of dispersion was determined once the cluster had been identified. When we examined the distance between consecutive locations, the likelihood a location was associated with a kill site declined as distance increased, with most of the consecutive locations ≤ 100 m apart being associated with a kill site (Fig. 4). No other temporal or spatial variables distinguished kill sites from non-kill sites. Surprisingly, habitat characteristics were similar between kill sites and non-kill sites (Fig. 5), indicating little preference among jaguars for the habitats in which they kill prey and habitats where they perform other activities, such as denning or social interactions.

Discussion

Dense vegetative cover, seasonal flooding (making travel difficult if not impossible) and the large area over which jaguars moved (Cavalcanti and Gese 2009) made the use of VHF radio-collars virtually impossible for determining predation sites in the Pantanal of Brazil. In fact, we initially radio-collared four jaguars with VHF radio-collars in 2000 and spent several months conducting intensive radio-tracking sessions using a null-peak system mounted on a vehicle, and attempted to locate and search for kills based upon the clustering of the radio-telemetry points. Given the inherent error of radio-tracking, our resulting clusters were so large that searching for prey remains became futile. We switched to GPS collars soon after they became commercially available in 2001, and for the first time, successfully determined kill rates and predation patterns for jaguars in South America (Cavalcanti and Gese 2010).

Accurate estimates of kill rates for large carnivores are now much more feasible with the development of GPS technologies (e.g. Tambling *et al.* 2010; Martins *et al.* 2011; Pitman *et al.* 2012; Miller *et al.* 2013). An ironic downside to the use of GPS collars is the abundance of locations acquired for each individual, and assuming many animals can be captured and radio-collared, researchers must wade through all of these data points. Anderson and Lindzey (2003) were two of the early researchers to recognise the need to systematically identify potential kill sites from all the clustered GPS locations received for an individual cougar. They found that the number of nights a cougar spent at a cluster was the best predictor for a large-mammal predation event, since most predation events occurred at night (Anderson and Lindzey 2003). Since this initial study, several researchers have developed various approaches to identifying clusters that have a higher probability of being predation sites (Webb *et al.* 2008; Knopff *et al.* 2009; Ruth *et al.* 2010; Tambling *et al.* 2010), with many different variables being found to be reliable predictors for discriminating kill sites from non-kill sites (e.g. Pitman *et al.* 2012; Miller *et al.*

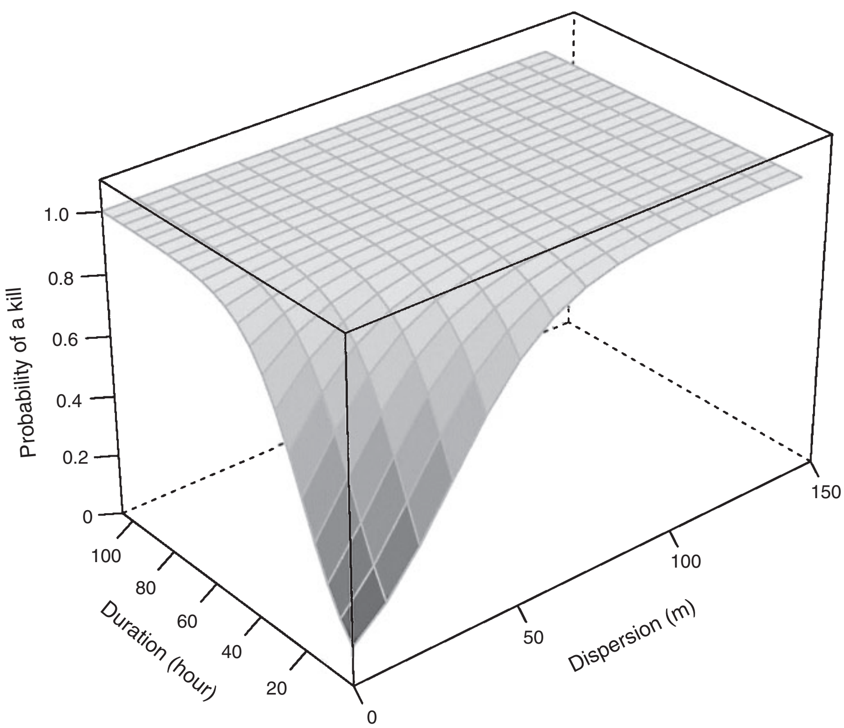

Fig. 3. Relationships among the duration of time a jaguar spends at a cluster, the dispersion of GPS locations around the cluster and the probability of the cluster being a jaguar kill, southern Pantanal, Brazil.

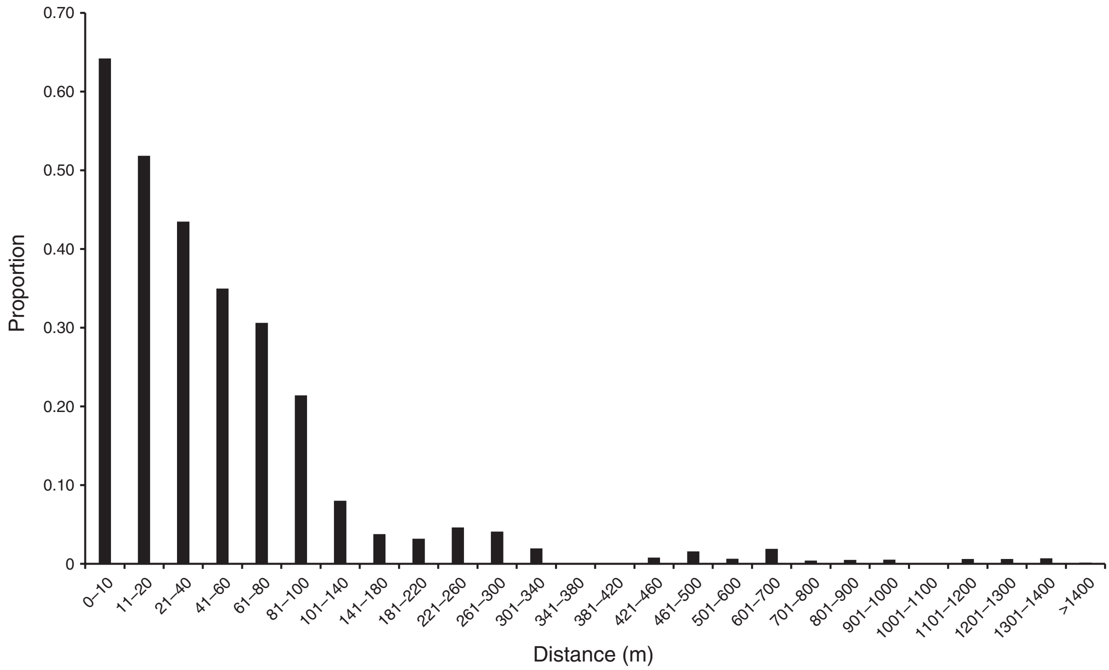

Fig. 4. Relationship between the distance (m) between consecutive locations and the proportions of consecutive locations that are associated with a jaguar kill site, southern Pantanal, Brazil.

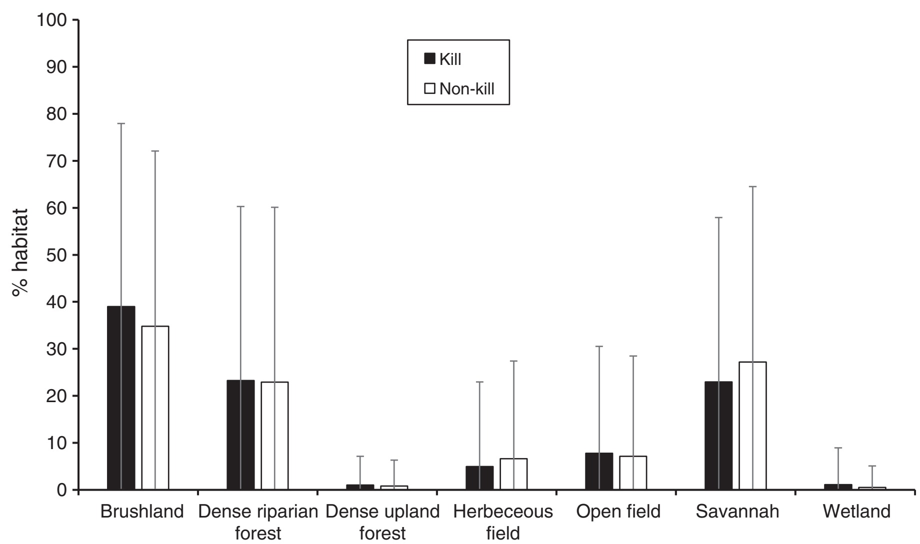

Fig. 5. Mean percentage (±s.d.) of seven habitat types amongst clusters identified as kill clusters or non-kill clusters for jaguars in the southern Pantanal, Brazil.

2013; Svoboda *et al.* 2013). Martins *et al.* (2011) reported that time spent at a given location by leopards (*Panthera pardus*) was positively related to the probability of detecting prey remains and prey size. Pitman *et al.* (2012) demonstrated that leopard predation could be modelled using GPS analysis and found that identified clusters were more likely to be kill sites at location clusters where the leopard spent more time, had dense cover, higher elevation, low levels of shrub cover and had more tree refugia present. Miller *et al.* (2013) showed that the top model for predicting Amur tiger (*Panthera tigris altaica*) kills included the duration of the cluster in hours and cluster fidelity. Similarly, Svoboda *et al.* (2013) found that clusters with more locations increased their odds of finding a bobcat (*Lynx rufus*) kill site. Krofel *et al.* (2013) used GPS cluster locations to find kill sites and den sites of Eurasian lynx (*Lynx lynx*), with 99% of the kill sites found at clusters longer than 30 h and with a minimum of two locations within 300 m.

Our research is the first attempt to use spatial, temporal, and habitat characteristics of potential clusters to identify jaguar kill sites in South America. We found that the duration of time a jaguar spent at the cluster, the number of nights a jaguar spent at a cluster and the dispersion of the points at the cluster were the best predictors of whether a cluster was associated with a kill. As the duration of time a jaguar spent at the cluster increased, the proportion of clusters that were associated with kills increased (Fig. 1*a*). This finding is not surprising given that jaguars spend a considerable amount of time at the kill, and they stay longer as prey size increases (Cavalcanti and Gese 2010). Similar to the duration of time at a cluster, as the number of nights a jaguar spent at a cluster increased, the more likely the cluster was associated with a kill (Fig. 1*b*). Finally, as the spatial dispersion of the cluster increased (i.e. the cluster increased in size), the proportion of clusters associated with a kill also increased (Fig. 2). The combination of duration at the cluster and dispersion of points was the best model for predicting the likelihood a cluster was a jaguar kill (Fig. 3). Again, we emphasise that the dispersion about the cluster was a different measure than the distance moved between consecutive locations. Similar to other studies, we did find that the probability of a location being associated with a kill site did decrease as the distance between consecutive locations increased (Fig. 4). Surprisingly, no habitat characteristics were important in determining whether a cluster was a kill.

Knopff *et al.* (2009) similarly found that cougar kills were more likely to be present at clusters that had a higher number of points, at clusters where the cougar was present for >1 day and at clusters where cougars showed high fidelity. Conversely to our finding of increased dispersion of points indicating a higher probability of a jaguar kill, Knopff *et al.* (2009) found that cougar kills were more likely to be found at clusters where the average distance from the geometric centre of the cluster was smaller. This contrast in the distance a cat remains from a kill may be due to the threat of kleptoparasitism to cougars from bears and wolves (Ruth *et al.* 2010; Krofel *et al.* 2012; Allen *et al.* 2014). Jaguars, as the apex predator, do not face such a threat. Anderson and Lindzey (2003) also reported that the probability of a cougar kill increased with the number of nights of cougar presence within a 200-m radius. Ruth *et al.* (2010) similarly found that the number of nights a cougar spent at a cluster was the most efficient variable at predicting a predation event, but cautioned investigators to ensure that kleptoparasitism did not influence predation rates in multi-predator ecosystems. Ruth *et al.* (2010) indicated that no cougar kills were missed when using GPS collar monitoring, but there were a few ($n = 16$) kills missed when using conventional VHF collar monitoring, due to small-bodied prey being consumed, kleptoparasitism of cougar kills by bears, wolves or other cougars, and when cougars left the kill site during the day. Because the jaguar is the apex predator in our study area, we believe their main rival, the cougar, likely did not attempt to usurp jaguar kills. Interestingly, the only indication that the main canid in the area (the maned wolf) was present on the study area, was when we found their remains after being depredated by a jaguar (Cavalcanti and Gese 2010).

Knopff *et al.* (2009) suggested that using GPS collar points to generate and examine clusters for kills and non-kills was most appropriate for carnivores that had high fidelity to kill locations, had long prey handling times and were a non-pack forming species. We found that jaguars spent more time at kills as prey size increased (Cavalcanti and Gese 2010) and generally travelled and hunted as a solitary animal (Cavalcanti and Gese 2009), thus making them an appropriate species for using GPS-based collars for predation studies. GPS collars provide not only more reliable estimates of kill rates and predation patterns for jaguars (Cavalcanti and Gese 2010), but also information on home-range size and overlap, social interactions, mating system and habitat use (Cavalcanti 2008). In addition, GPS collars can provide data on movement distances, which are useful for estimating population density when combined with remote camera trapping (Soisalo and Cavalcanti 2006), as well as information on denning behaviour (e.g. Krofel *et al.* 2013). The only disadvantages of GPS collars may be the initial costs and the bias for large prey when the relocation acquisition schedule of the GPS collars is temporally far enough apart between locations that small prey items are completely consumed in that time interval, and therefore no cluster is identified for investigation in the field. As GPS and battery storage technology improves, perhaps lighter and longer-lasting batteries will allow for shorter time intervals between location fixes without sacrificing long-term battery life of the collar. Future studies with longer-lasting battery life will likely be able to have shorter time intervals between locations and more frequent downloads of GPS data, providing the opportunity to find kill remains of smaller prey.

In conclusion, we found that the time of duration a jaguar spent at a cluster and the dispersion of points around the cluster were reliable predictors of whether a GPS cluster was a jaguar kill. Hopefully, as the costs of GPS collars decrease, the ability to capture and collar more individuals will provide for greater detail on predation patterns, including identification of smaller prey species. However, as the number of collars on a study increases, so too does the time and effort needed to investigate all possible clusters identified. Our results will assist future researchers examining kill rates and predation patterns of jaguars, allowing for more efficient use of time and personnel by reducing the number of clusters requiring investigation in the field. Due to the lack of topography in the Pantanal, future studies in more mountainous terrain will likely need to incorporate other habitat variables (e.g. slope, aspect, elevation) into their models for discrimination among clusters to distinguish potential jaguar kill sites from non-kill sites.

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