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Home range size, movement, and habitat use of yellow anacondas (*Eunectes notaeus*)

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Abstract. Movement ecology is an important tool for understanding animal behaviour toward basic needs, as well as to design conservation and management priorities. Animals usually do not move randomly and may prefer certain types of habitats over others. The yellow anaconda (*Eunectes notaeus*) is one of the largest snakes in South America. However, little is known about its natural history. Here, we present results from a telemetry study to quantify movement patterns and habitat use of eight yellow anacondas in a protected, seasonally flooded area in Midwestern Brazil. Yellow anacondas were associated to small channels with macrophyte stands and bushy vegetation. They moved relatively little (188 m monthly) and had small home range (mean 6.2 ha); they used native pastures and abandoned farmlands with forest patches more than expected by chance. Our results contribute to the understanding of dispersal patterns, habitat choices, and life history of this large aquatic snake and to the body of knowledge needed for management and conservation of its populations and habitats.

Key words. Squamata, Serpentes, Boidae, home range, wetland, landscape ecology, South America.

Introduction

Studies of animal movement have a long history, but recently they attracted enormous attention, because of advances in tracking technology and analytical methods (Kays et al. 2015). Clearly understanding animal movements is crucial to establish management priorities in undeveloped areas with high diversity (Van Moorter et al. 2016). To understand individuals' movements and how they might connect habitat selection and home range, we need to examine a wide range of life-history trade-offs and environmental variability (Nathan et al. 2008). Thermoregulation and weather conditions (i.e. temperature, relative humidity, and wind speed) (Moore & Gillingham 2006, George et al. 2015), foraging, local seasonal migrations, and mating (Rivas 2015) highly influence snake movements and habitat choice.

Large snake species can act as top predators in aquatic and terrestrial ecosystems (Headland & Greene 2011, Miranda 2017), and move in response to prey movements (King & Duvall 1990, Sperry et al. 2013). There is evidence that individual movement rates and home range are positively correlated with body size (Perry & Garland Jr 2013, Bastille-Rousseau et al. 2016). Vagile snakes with large home ranges often cross disturbed habitats, which makes individuals more vulnerable to predation or anthropogenic mortality, such as intentional killing or roadkill (Bonnet et al. 1999, Jochimsen et al. 2014). Studies with relatively large snakes have registered huge home ranges – for both ambush and active foragers – but they also pointed a large individual variation in the home ranges. For example, Marshall et al. (2019) registered for king cobra an average of 493 ha (51–802), while Burmese python has an average home range of 2250 ha (20–8740; Hart et al. 2015). However, the two anaconda species studied so far seem to be more sedentary, with a home range varying between 6.7 and 37 ha (Rivas 2015, De La Quintana et al. 2017).

Anacondas (*Eunectes* spp.) comprise a group of large constricting snakes, widely distributed in tropical and subtropical areas of South America (Dirksen & Böhme 2005). However, information on the natural history of the four species of anacondas, particularly on home range and movement patterns, remains limited and biased towards green anacondas (*E. murinus*; Rivas et al. 2007, 2016, De La Quintana et al. 2017), and Beni anacondas (*E. beniensis*; De La Quintana et al. 2017). Studies on yellow anaconda (*Eunectes notaeus*) show that it is a generalist predator closely associated with freshwater wetlands of the La

Plata basin (McCartney-Melstad et al. 2012, Santos et al. 2013, Miranda et al. 2017). Evidence about population structure and gene flow from Argentine Humid Chaco yellow anacondas showed a sex-biased dispersion. Moreover, they showed that the configuration of rivers and surrounding habitats, like floodplains and small creeks, was important to explain the spatial structure of populations (McCartney-Melstad et al. 2012). Furthermore, close association with aquatic-terrestrial transition zones or permanently flooded areas seems important because of thermoregulatory constraints, such as preventing exposure to extreme critical thermal temperatures (Strüssmann & Sazima 1993, McConnachie et al. 2011).

Some populations have been exploited for multiple uses, such as food, leather industry, ornamentation, and medicinal practices (Micucci & Waller 2007, Alves et al. 2012), and gene flow among populations may be impaired for natural or anthropogenic reasons (McCartney-Melstad et al. 2012). In the Brazilian portion of the Pantanal – the largest tropical wetland – yellow anacondas are intentionally killed to protect livestock, and alterations in flood dynamics associated to land use change in upland habitats of Pantanal may also be a threat to this large and poorly-known predator (Miranda et al. 2016, Roque et al. 2016).

Using radio telemetry, we evaluated home range, habitat preferences, and movements of the yellow anaconda in the northern part of the Pantanal ecoregion. We focused on the following questions: i) how large is the home range and how far does an anaconda move? ii) what kind of habitats yellow anacondas use? We expected that individuals select the locations close to permanent wetlands, because they largely depend on resources from aquatic environments. In addition, we discuss issues on tracking a large semi-aquatic snake.

Methods

Study area

We conducted our fieldwork at the Serviço Social do Comércio Pantanal Natural Heritage Private Reserve (hereafter SESC Pantanal; 16°51'50"S, 56°23'19"W), a particular protected area located in the floodplain of the Cuiabá River (state of Mato Grosso, Brazil) that also is recognized by the Ramsar Convention. The reserve has an area of 1,070 km² and includes a mosaic of freshwater environments (ephemeral and permanent ponds, channels, and flooded areas), grasslands, savannas, and dry forests. Annual flood events are common in the rainy season (December to March) due to river overflow and rainfall runoff. As in most areas of the Pantanal ecoregion, SESC Pantanal has a homogeneous topography with low lying relief (120–131 m a.s.l.), and micro topography is an important factor for local flooding patterns (Girard 2011). Flood beginning is characterized by appearance of distinct aquatic environments (rain puddles, shallow flooded areas, temporary ponds) that are not necessarily connected with rivers or permanent ponds. During the steady flood period, the floodplain is almost completely covered by surface water (varying from 50 cm to 300 cm), except for paleo-levees with higher elevation (1–3 m above flood level). In the drawdown period, natural drainage channels and floodplain ponds are largely disconnected from the river channel/permanent ponds. So, hydroperiod is quite variable, depending on flood intensity. During the dry season, many ponds dry out completely, except for scattered permanent ponds and small drainage channels, and are subject to sporadic fires.

Small-scale variation in vegetation types is closely related to soil properties and hydrological conditions (Junk & Nunes da Cunha 2012). So, local vegetation types do not show a clear distinction between woody and grassy formations, although grasslands are more common in areas with higher flood duration and different types of forests occur at intermediate flood levels. Grasslands comprise a mosaic of native and exotic grasses, such as *Imperata brasiliensis, Axonopus purpusii, Elyonorus muticus, Paspalum carinatum*, and *Urochloa humidicola.* Monodominant stands composed by *Vochysia divergens*, locally known as cambarazal, are common in riverine forests and areas with high flood duration (5–6 mo). However, cambarazal has spread vigorously in abandoned pastures of the Pantanal. Dense arboreal savannas (a mix of dry forests and closed woodlands) occur in rarely or permanently non-flooded areas and are composed mainly of *Anadenanthera colubrina*, *Tabebuia ochracea*, and *Curatella americana* (Brandão et al. 2011). An extensive cattle ranching was the major land use until the creation of the SESC Pantanal reserve in 1997. Cattle access is not allowed since then, although sporadic cattle grazing may occur at reserve borders. In addition to extensive grazing, ecological integrity of the wetlands in the reserve has been affected over time by fire, as well as by regulation of the Cuiabá River for hydropower generation (Zeilhofer & de Moura 2009, Brandão et al. 2011).

Snake captures and transmitter implantation

We captured anacondas at the end of dry season in 2015 (October and November). Most individuals displayed a number of injuries and scars (bite marks, burns, and tail loss; Supplementary Fig. S1). Anacondas are inconspicuous snakes and difficult to find in the aquatic environments of the Pantanal during the floods; however, this becomes easier as the water in the floodplain recedes and these snakes move to the remaining ponds or channels. The area sampled at the SESC Pantanal included 18 permanent wetlands, such as ponds and small channels (Fig. 1). Yellow anacondas were located by active search mainly during the day, but night searches using flashlights were also performed. Teams of three to five people waded through shallow water probing aquatic vegetation and water with feet or sticks (Rivas et al. 2007). After detection, snakes were captured by hand and restrained by putting a cotton sock over the head before further processing (Rivas et al. 1995). We recorded capture locations using a handheld GPS unit. All individuals were measured (snout–vent length – SVL, and total length – TotL) using a string to follow the middle line of the body (Rivas et al. 2008), weighed, sexed, and marked with passive integrated transponder tags. Suitable individuals (TotL > 1.80 m and body mass > 2.5 kg) were kept in captivity for surgical implantation of transmitters.

We captured *E. notaeus* during 220 person-hours of searching. All snakes were found during daytime in aquatic environments (mean depth of 29 cm and mean water temperature of 27.1°C), entirely submerged or with part of the body out of the water among floating vegetation. Eight snakes (six females and two males, hereafter treated as ID 1–8) were implanted subcutaneously with a VHF transmitter and GPS receiver coupled in a single device < 3.2% of snake body weight (dimensions 60 × 30 × 10 mm, whip antenna 200 mm, weight 80 g; Tigrinus Equipamentos para Pesquisa Ltda., Santa Catarina, Brazil). Surgeries were made at the Veterinary Hospital of the Universidade Federal de Mato Grosso (UFMT, Cuiabá, Mato Grosso, Brazil), under isoflurane inhalational anaesthesia. The telemetry device was positioned laterally in the posterior third of the snake's body. Sutures with nylon threads were used to close the incision. During the recovery period, they were kept in captivity in individual enclosures and received local and systemic antimicrobial therapy to prevent infection. Anacondas were released at the place of capture 7–10 days after surgery.

Telemetry survey and habitat categories

Anacondas shelter in dense vegetation or underground in burrows, therefore the fix (i.e. GPS location) success rate of receiver may be compromised and more battery will be used. In this sense, GPS receivers were programmed to record locations every four hours with a time-out period of five minutes for fix acquisition, and battery life span was estimated to last 12–13 months. Data points were downloaded after each transmitter was recovered. In a dry run, we used GPS in different simulated conditions (underwater, inside a fish, buried, etc.) and found that the GPS gathered about 60% of expected data in environmental conditions similar to the study site. It failed to gather information only when buried.

When satellite and VHF radio telemetry are used jointly, VHF component is not used only for data acquisition, being critical for the retrieval of data stored on GPS tags. So, our tracking protocol was designed to minimize interference on snake's behaviour and also to avoid signal loss of individuals that could move out of range of the radio. We radio tracked anacondas from November 2015 to October 2016 in monthly expeditions of seven days each. Each individual was located approximately every 56 h (55.8 ± 8.4) by expedition. We limited radio tracking intervals between

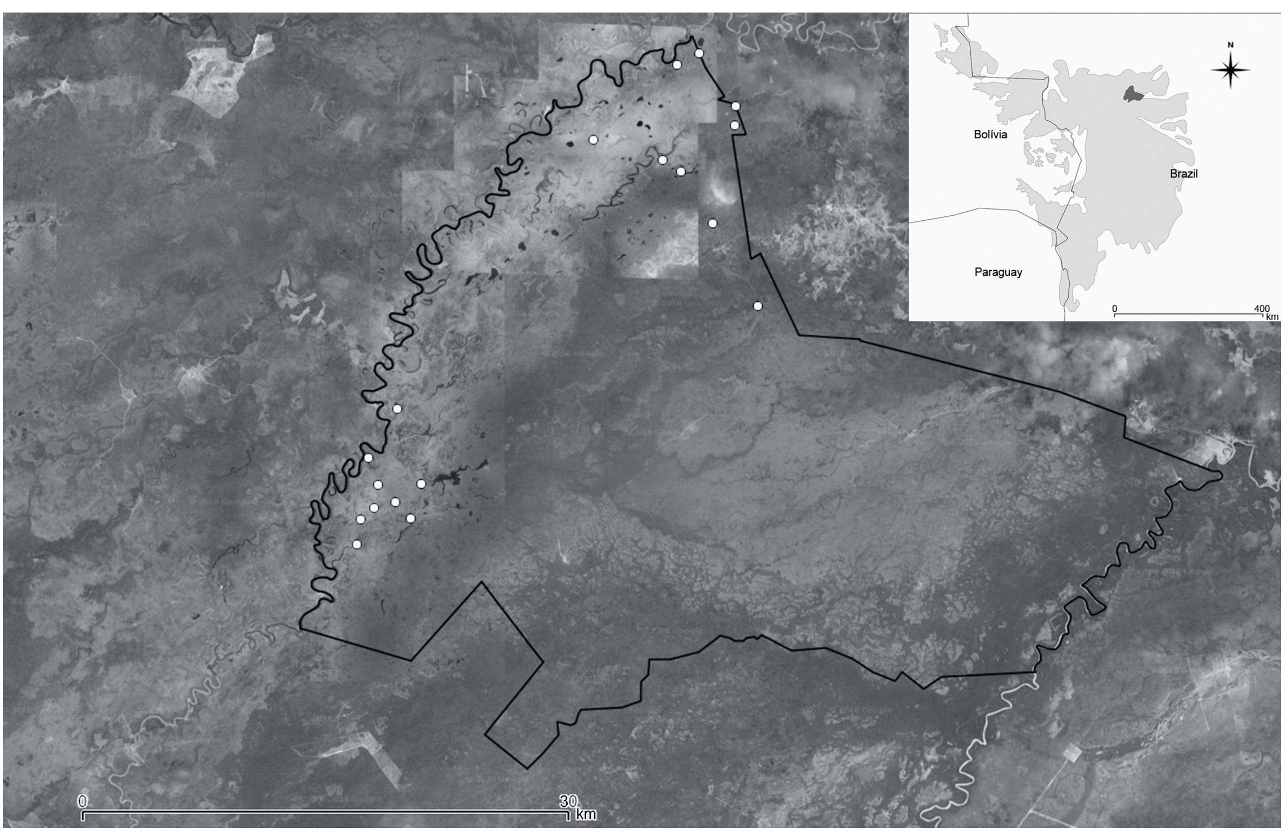

Figure 1. Map indicating the location of Pantanal ecoregion (inset map, dark grey area) and wetlands sampled (white circles) where eight yellow anacondas were radiotracked in the SESC Pantanal reserve (polygon, naturally limited by the Cuiabá River – left – and São Lourenço River – right), Brazil.

Table 1. Type of wetland and microhabitat used by *Eunectes notaeus* radio-tracked in the private reserve SESC Pantanal, Brazil, between November 2015 and October 2016. Values correspond to number of locations by individual (% locations). Depth corresponds to the mean of water depth from all individual localizations.

	Wetland			Microhabitat				Water depth (m)
ID	Ponds	Small channel	Flooded areas	Open water	Macrophyte stands	Grasses	Bushes	
1	0	7(100)	0	4(57.1)	1(14.3)	2(28.6)	0	1.7
2	0	2(25)	6(75)	2(25)	0	0	6 (75)	1.6
3	1(6.2)	15(93.8)	0	13(81.3)	3(18.7)	0	0	2.0
4	7(100)	0	0	0	7(100)	0	0	0.4
5	0	12(100)	0	1(8.3)	11(91.7)	0	0	2.1
6	0	3(23)	10(77)	0	2(15.4)	1(7.6)	10(77)	1.5
7	5(45.5)	0	6(54.5)	0	5(45.5)	0	6(54.5)	0.9
8	3(60)	0	2(40)	0	3(60)	1(20)	1(20)	0.4
Total used	16(20.2)	39(49.4)	24(30.4)	20(25.3)	32(40.5)	4(5.1)	23(29.1)	–

09:00–17:00. Tracking was performed mainly on foot with locations recorded using the handheld GPS unit, although a boat was necessary during the flood peak. When direct observation was not possible, the position of the snakes was determined using a small unidirectional antenna surrounding the source of the maximum signal. Even if an anaconda could not be seen, its location could be determined within an area of 20 m².Once located we recorded whether the snake was visible or not, water depth, type of wetland (pond, small channel, or flooded area), and microhabitat (open water, macrophyte stands, grasses, and bushes; see Table 1). Locations taken from an airplane were occasionally used when the animals had gone too far or the habitat prevented us from following the animal. In this case, we typically searched for individuals from altitudes around 400 m and as soon as a signal was received we approached this spot from several directions to pinpoint a location.

To visualize movement patterns, we assumed linear movement and created tracks by connecting successive points using the adehabitatLT package (Calenge et al. 2009). Estimates of home range (HR) were based on 100% Minimum Convex Polygon (MCP) using the adehabitatHR package (Calenge 2006) in R (version 3.4.3; R Foundation for Statistical Computing, Vienna, Austria, see www.R-project.org). To assess macrohabitat use, we overlaid the individual home range maps onto the SESC Pantanal land-use maps using QGIS 2.18.16 (QGIS Development Team 2018). The study area was classified into four broad macrohabitat types: native grasslands, abandoned farmlands with forest patches (mixed exotic pasture occupation associated with monodominant stands), mosaic of dense arboreal savannas, and mosaic of native grasslands and exotic pastures. We based our category allocation on Google Earth imagery, using a land-cover classification for 2014 developed by Brazilian Institute of Geography and Statistics (IBGE 2017).

We estimated macrohabitat availability as the proportion of each land use type within the study area (a circular buffer with a 3000 m radius) from LANDSAT imagery, using QGIS. We used a Fisher's two-tailed exact test (Siegel & Castellan 1988) to compare the observed use of macrohabitat with the available macrohabitat under the null hypothesis that there was no preference for the macrohabitat type the snakes used. Home range of one anaconda (ID 4) was not included in the macrohabitat availability analysis because it was far from the remaining anacondas (~ 25 km) and the habitats available for it were very different.

Results

We monitored the yellow anacondas for 218 days, gathering a total of 79 locations from all eight snakes in the field. Animals 1, 2, and 4 were lost and their signal could not be heard even after two monitoring flights (September and October 2016). In the other five cases, attempts to locate snakes revealed only the transmitters on the ground without any signs of a snake carcass nearby (ID 3, 5, 6, 7, and 8) during the final part of the monitoring. Only one GPS data logger contained stored locations (ID 6) with 50 points. Because these GPS points did not add new peripheral points for home range estimates, we used only VHF data for estimates of home range and movement patterns for all individuals.

During the monitoring period, the average air temperature was 33°C (21.5–45) and water temperature was 29.8°C (21.5–40). Anacondas were found mostly in the water (94.9%), among macrophyte stands (40.5%) or flooded areas with bushy vegetation (29.1%) at a mean depth of 1.3 m. Anacondas were in ponds 20.2% of the time, 49.4% in small channels, and 30.4% in flooded areas (Table 1). During the study, only two of the radio-tracked snakes were sighted basking or swimming in small channels (Fig. 2). Of the 79 locations, in only three there was a direct observation of the individual, with the visual detection probability of a snake at < 5%.

Yellow anacondas have a mean monthly movement of around 188 m (Tab. 2). Of the eight tracked anacondas, the maximum monthly distance travelled was 900 m for females (December) and 691 m for males (March). However, three "nomadic" females moved three to four times more than other anacondas followed during this study (ID 3, 7, 8; Table 2). The majority of the tracked anacondas remained inside the permanent wetlands where they had been captured, but one female (ID 8) moved into an oxbow lake of the Cuiabá River (Supplementary Fig. S2). Individual home ranges overlapped in three cases, between a female and a male (ID 1 and 2, ID 5 and 6) and between two females (ID 7 and 8).

Home ranges calculated from MCP varied between 0.1 and 17.7 ha (Table 2). The three "nomadic" females had home ranges greater than 10 ha, while home ranges of the remaining five anacondas varied between 0.1 and 2.3 ha. Although most anacondas were radio-tracked for less than eight months, small home ranges did not seem to be related to short monitoring period (Table 2). Within individual home ranges, anacondas used areas of native grasslands and abandoned farmlands with forest patches (Fig. 3). Only one individual was tracked in a mosaic of native grasslands/exotic pastures (Table 3). Native grasslands were used substantially more than expected (observed: 56; expected: 41.8; two-tailed Fisher's exact test; $p = 0.006$; Table 3).

Discussion

Our results show that yellow anacondas are strongly dependent on aquatic habitats, using small channels and relatively shallow waters with macrophyte stands and bushy vegetation. Yellow anacondas were sedentary, even during the flood season, suggesting some fidelity to permanent wetland boundaries. Small to moderate home range sizes for large species are often associated to high food availability. This is particularly common in generalist predators, including reptiles living in floodplains (Brown et al. 2005, Fujisaki et al. 2014, Walters et al. 2016). Other factors that may influence movement are thermoregulation needs, avoidance of predators, mating and other social interactions (Bruton et al. 2014, George et al. 2015, Zappalorti et al. 2015). However, the sampling period was just after the mating season – which occurs at the end of the dry season (Waller et al. 2007) – so mating was not likely an important driver at this time.

Whilst our findings provide evidence that yellow anacondas have small home ranges, we are limited in the scope of our conclusions given the short sampling period (primarily 6–8 months), and the few (5–16) relocations by tracking with VHF due to the failure of the GPS tags. So, direct comparisons of movement rates should be made with caution. The use of burrows, underwater habitats, or shelters amidst thick vegetation hamper GPS performance and may resulted in the failure of the GPS transmitters (Frair et al. 2010). Moreover, from the eight transmitters implanted, three were not recovered. The other five were found left in the field. While it is possible that the five associated ana-

Figure 2. Some of the individuals of yellow anacondas (*Eunectes notaeus*) radiotracked during the study: A) male coiled on a macrophyte raft; B) female being inspected for signs of infection and inadequate healing; C) female found swimming among aquatic vegetation.

Table 2. Individual characteristics, days and numbers of locations (VHF data only), and movement data for eight yellow anacondas (*Eunectes notaeus*) radiotracked in SESC Pantanal, Brazil, between November 2015 and October 2016. TotL: Total length, SVL: Snout–vent length.

ID	TotL (m)	SVL (m)	Mass (kg)	Sex	Monitored days	Number of locations	Mean monthly distance (m)	Total distance travelled (m)	Home range (ha)
1	1.97	1.76	4.5	Male	179	7	30.1	182.1	0.3
2	2.85	2.62	12.8	Female	181	8	106.2	641.1	2.3
3	2.68	2.45	11.5	Female	217	16	296.5	2078.3	17.7
4	2.63	2.43	11.1	Female	88	7	105.25	207.4	0.6
5	2.10	1.87	5.0	Female	295	12	30.4	122	0.1
6	1.92	1.77	3.6	Male	206	13	160	767.2	0.7
7	3.57	-	21.2	Female	288	11	301.7	1699.5	16.4
8	3.36	-	11.1	Female	292	5	474.8	4281	11.2
Average	2.6	2.15	10.1		218	10	188.1	1247.3	6.2

Table 3. Macrohabitat used by *Eunectes notaeus* radiotracked in the private reserve SESC Pantanal, Brazil, between November 2015 and October 2016. Values correspond to number of locations (% locations).

ID	Native grasslands	Mosaic native grasslands/ exotic pastures	Abandoned farmlands with forest patches	Dense arboreal savannas
1	7 (100)	0	0	0
2	8 (100)	0	0	0
3	15 (93.7)	0	1 (6.3)	0
4	0	7 (100)		0
5	12 (100)	0	0	0
6	13 (100)	0	0	0
7	0	0	11 (100)	0
8	1 (20)	0	4 (80)	0
Total used	56 (70.9)	7(8.9)	16(20.2)	0

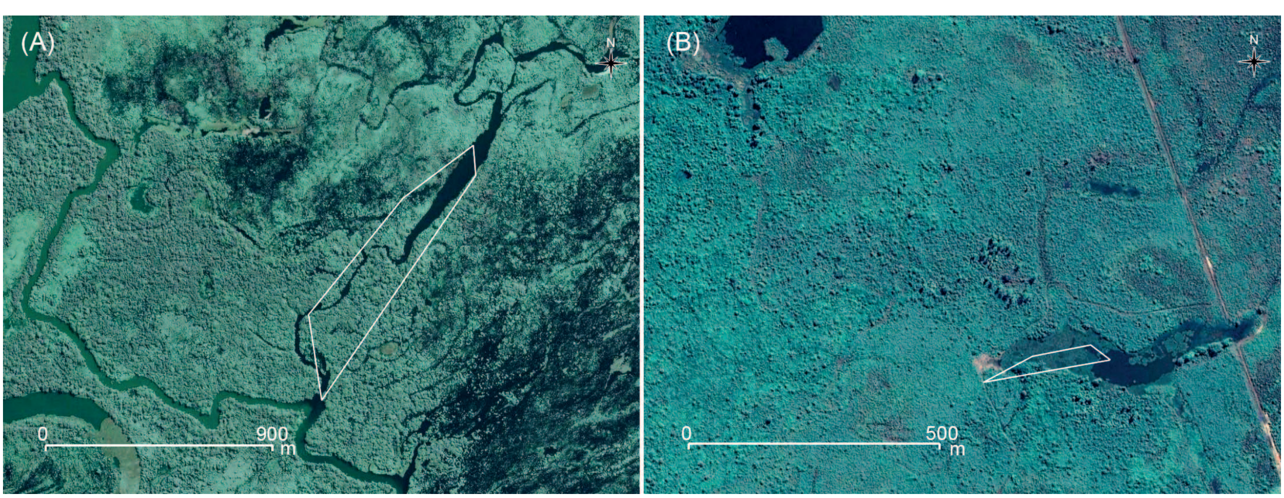

Figure 3. Aerial views with minimum convex polygon (100%) areas of two radio-tracked anacondas, showing home ranges at different land uses in the SESC Pantanal, Brazil. A) Individual (ID) 3 using natural grassland and forest patches. B) ID 4 using mosaic of native grasslands/ exotic pastures. Numbers correspond to the ID in Tables 1 and 2.

condas have died and were subsequently scavenged, leaving only the transmitter in the field, no traces of carcasses were found nearby. Furthermore, former studies have documented that internal transmitters can be expelled in faeces or through the body wall (Pearson & Shine 2002, Smith et al. 2018). Thus, we have no way to discern what happened to these snakes.

Our results are consistent with previous findings of *E. murinus* habitat preference in Venezuela, and *E. beniensis* in Bolivia. Both species preferred shallow water with abundant aquatic vegetation (Rivas 2015, De La Quintana et al. 2017). Home ranges here reported for *E. notaeus* are also similar to those for *E. beniensis*, which have a home range between 6.7–39.4 ha (De La Quintana et al. 2017), and *E. murinus*, with a home range of 0.01 to 37 ha (Rivas 2015). A study in northern Argentina with *E. notaeus* also found a comparable home range (15–50 ha; Natusch et al. 2017). The somewhat smaller home range found in this study can be explained by the short time of the study, which was limited to only one rainy season and one dry season. However, long periods of inactivity and reduction of home range sizes (home range < 0.4 ha) were reported under suboptimal conditions or during pregnancy (Rivas 2015, De La Quintana et al. 2017). In fact, most of the females in our study, with the exception of ID 8, presumably had enough fat reserves to have been breeding (Rivas 2015), so the low mobility could be a result of the females likely being pregnant (Rivas 2015).

Eunectes notaeus is an ambushing or foraging predator and feeds most commonly on wading birds and shorebirds (Strüssmann 1997, Miranda et al. 2017, Camera et al. 2019), which are reduced during flooding periods (Figueira et al. 2006, Donatelli et al. 2014). Subsequently, aquatic predators, such as the giant otter (*Pteronura brasiliensis*, Mustelidae) and caimans (*Caiman yacare*, Alligatoridae) take advantage of flooded grasslands and forests in the areas adjacent to rivers (Leuchtenberger et al. 2013, Campos et al. 2015). The great number of scars observed in the anacondas captured for the study could be caused either by defensive efforts of prey or from predator attacks (Rivas, 2007).

The benefits of using shallow aquatic habitats may be also responsible for the small home ranges registered here. By spending long periods partially submerged and coiled in shallow waters, yellow anacondas can reduce thermoregulatory costs because the average water temperature is usually high (McConnachie et al. 2011). This may reduce the odds of predation. In addition, floating and rooted vegetation may provide both microhabitat for foraging aquatic birds and camouflage for anacondas (see Fig. 2). With regard to the overall macrohabitat choice, the apparent preference for open land cover may be attributed to variation in water availability. In Pantanal, dense arboreal savannas are established in patches of drier terrains that become flooded only for a few days or weeks, or that does not flood at all. In Bolivia, *E. beniensis* seems to have a similar tendency, avoiding forested areas with little availability of permanent wetlands (De La Quintana et al. 2017).

Although GPS telemetry has advantages in studies with large constrictors (Smith et al. 2018), we unfortunately experienced issues of equipment failures and loss of transmitters. In light of these issues, we highlight that the choice of transmitters should be done with caution. For aquatic and semi-aquatic snakes, we suggest the use of VHF component of GPS transmitters for joint data acquisition.

In conclusion, we showed that individuals of *E. notaeus* select native grasslands; their home ranges are relatively small, and closely associated with permanent wetlands, both in dry and in rainy seasons. Our results add valuable information about life history and ecology of *E. notaeus*, and are a key step to help to fill knowledge gaps on this poorly understood large snake.

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Supplementary data

The following data are available online:

Supplementary document S1. Some injuries found in the radio-tracked anacondas in the SESC Pantanal.

Supplementary document 2. Map showing the home ranges for eight yellow anacondas tracked in the SESC Pantanal.