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INTER-TROPHIC FOOD PROVISIONING BETWEEN SEA AND LAND: THE JAGUAR (*Panthera onca*) AS PROVIDER OF SEA TURTLE CARCASSES TO TERRESTRIAL SCAVENGERS

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Abstract

A more complete perspective of carrion use by terrestrial vertebrates and about the role of predators in net carrion supply will improve our understanding of critical ecological processes, particularly those associated with energy flow and trophic interactions. Therefore, the aims of this work were: 1) to record the scavenger species which are benefited indirectly by the predator-prey relationship between jaguars and sea turtles, and 2) to evaluate the influence of activity of vultures on the feeding behavior of the jaguar on sea turtles. During the study period a total of 24 predation events on sea turtles by jaguars were recorded at Nancite beach, Costa Rica. We recorded a total of 11 vertebrate species scavenging on sea turtle carcasses. In this paper, we found that the number of days that the jaguars fed on a sea turtle carcass was correlated with the number of days that the vultures took to find the sea turtle carcass. Our work concluded that the ecological value of jaguars as a top predator, flag, umbrella and keystone species includes their role as a provider of carcasses to scavengers.

Keywords: *Carrion subsidies; Competitive behavior; Kleptoparasitism; Trophic interactions; Scavenging behavior; Vulture activity; Predation links.*

Introduction

In most of the classical ecology textbooks and scientific manuscripts related with food webs, nutrient cycling, energy flow, and trophic interactions, the ecological value of scavenging links is underestimated. Also, the fact that the energy transferred via scavenging substantially exceeds that of predation has frequently led to the inflation of predation impacts and the underestimation of indirect effects of scavenging [1, 2]. More recently however, several textbooks and review papers have highlighted the growing body of evidence supporting the essential role of carrion and scavenging in trophic ecology [1-8]. Scavenging ecology now has a considerable body of theoretical and empirical evidence supporting its ubiquitous, nonrandom, high-magnitude energy-transfer pathways, with wide implications from the individual to the population, community, and ecosystem level, with close connections to other ecological processes and ramifications for other scientific disciplines [5-8]. For example, a single large vertebrate carcass in a terrestrial ecosystem (i.e., forest or savannah) may support scavenging across multiple trophic level consumers such as apex predatory mammals (e.g., bears, wolves,

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lions), secondary mammalian consumers (e.g., small carnivorous rodents, foxes, hyenas), as well as air-borne consumers (e.g., eagles, hawks, vultures, insects) [2]. Despite significant advances in the knowledge of ecology, the scientific community is far from recognizing and understanding all the direct and indirect trophic interactions related with scavenging [2, 6-8]. The description of the links among preys, predators and scavengers is needed to improve scavenging knowledge and current energy flux models [1, 6, 9].

One of the most important large predators in Latin America is the jaguar, which is considered an apex predator. The top predators have the potential to control prey abundances and also mesopredator populations [10]. It has been widely stated that the disappearance of apex predators could lead to secondary extinctions [11], which makes them especially important for achieving conservation goals. In fact, the jaguar could be regulating population densities of mammals which consume seeds of the enormous tropical trees [12], this associates the jaguars with the structure of the forest. Furthermore, the jaguar has a large number of prey species [13], therefore, it could be associated with multiple trophic interactions.

Throughout Latin America, jaguars have been recorded killing four species of sea turtles on its nesting beaches [14-27]. The knowledge about this relation has increased considerably in recent years, especially in terms of the temporal and spatial trends of jaguar predation [22, 27], carcass utilization rates [14, 15] and the impact on sea turtle populations [15]. However, an aspect totally unknown is the scavenging ecology of this trophic interaction [15]. For example, investigations are required to determine the effects that vertebrate scavenging may have on jaguar return rates to sea turtle carcasses [15]. Therefore, the aims of this work were: 1) to record the scavenger species which are benefited indirectly from the predator-prey relation between jaguars and sea turtles, and 2) to evaluate the influence of the activity of vultures on the feeding behavior of the jaguar on sea turtles.

Materials and Methods

Study site. Santa Rosa National Park is located in the Guanacaste Province, Northwest Pacific coast of Costa Rica. It has an extension of 38,628 ha and is part of a continuous biogeographic block of 163,000ha of protected land within the Guanacaste Conservation Area. Santa Rosa National Park protects one of the best-preserved dry forests of Central America. Within this park there are several important sea turtle nesting beaches (e.g. Naranjo, Colorada, Nancite, Isla San Jose, Potrero Grande, among others). One of the most important of these is Nancite, which is located in the southwestern part of Santa Rosa National Park (10º48´N and 85º39´W; Fig. 1); Nancite has a length of approximately 1050m and preserves mainly coastal-marine ecosystems (besides mangroves, lagoons and dry deciduous and semi-deciduous forests). Nancite has been fully protected from intrusive human activities, including tourism. This beach is well known for the Olive Ridley arribada phenomenon, which consists of the massive synchronous nesting of hundreds or thousands of Olive Ridley over a few consecutive nights [28-30]. Arribadas also occur at a second beach in Costa Rica (Ostional) and selected beaches in Mexico, India, Nicaragua (La flor and Chacocente), and Panamá (Isla Cañas) [29].

Methods. Jaguar predation was assessed through morning surveys on Nancite beach, as part of a jaguar-sea turtle research project of the National University of Costa Rica. The morning surveys were made between August 1st and December 1th 2015; all jaguar-predated turtles were recorded. We set up camera traps on every freshly predated sea turtle that we found (Fig. 2). We distinguished the jaguar predated turtles from those killed by other predators (like crocodiles or humans) by a set of distinctive characters such as bite marks on the turtle's neck and front flippers, tracks around the kill or if the kill had been dragged inside the beach vegetation [11, 16]. For every predation event the following variables were recorded: a) species of vertebrate scavengers that fed on the sea turtle carcasses, b) number of days that the jaguars fed on the sea turtle carcasses, c) number of days that the vultures took to find and fed from the sea turtle carcasses, d) distance in meters that the jaguar dragged the sea turtle carcasses from the beach to the forest, and e) carapace length of sea turtle that was predated (see Appendix A). We used the Spearman Rank Correlation to analyze the relationship among the different variables recorded at predation events. Linear models were made to quantify the effect among the different variables recorded on the predation events. All statistical analyses and graphics were performed using R language with Rcmdr interface [25].

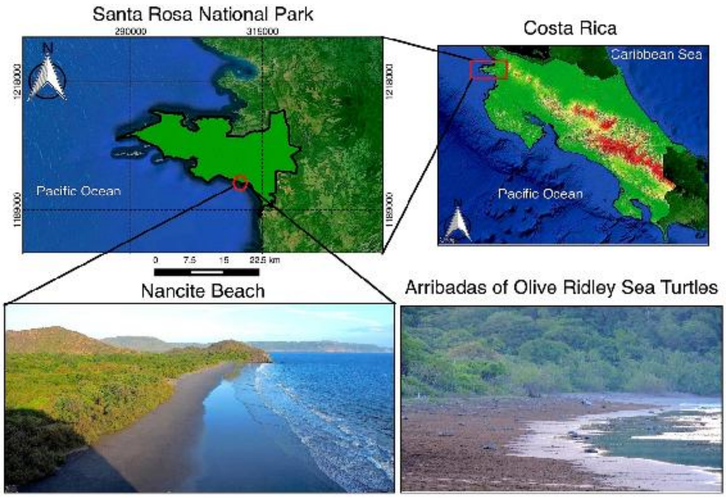

Fig. 1. Location of Nancite Beach, Santa Rosa National Park, Guanacaste Province, Costa Rica. Nancite Beach is an important rookery where Olive Ridley sea turtle (*Lepidochelys olivacea*) aggregate to nest synchronously during arribadas.

Fig. 2. Jaguar (*Panthera onca*) feeding of the olive ridley sea turtle carcasses (*Lepidochelys olivacea*) at Nancite Beach, Santa Rosa National Park, Costa Rica. Photo Luis G. Fonseca

Results

Scavengers of the sea turtle carcasses. During the study period, we recorded a total of 24 predation events on sea turtles by the jaguar at Nancite beach. Of these predation events, 20 (83.3%) were on olive ridley sea turtle (*Lepidochelys olivacea*) and four (16.6%) were on the green sea turtle (*Chelonia mydas*). We recorded a total of 11 vertebrate species scavenging on the carcasses. These vertebrate species are distributed in three classes, seven orders, nine families and 11 genus (Table 1). Of the 11 species recorded, the black and turkey vulture were the most frequent scavengers followed by the common opossum *Didelphis marsupialis* (Fig. 3).

Table 1. Vertebrate species that fed on sea turtles predated by jaguar, at Nancite Beach, Santa Rosa National Park, Costa Rica

TAXA	Carcasses visitation	Register type	Reference
MAMMALIA			
CARNIVORA			
Canidae	1		
Canis latrans (Coyote)		Pers. Obs.	No picture recorded
Felidae			
Puma concolor (Cougar)	1	Camera trap	Appendix C
Procyonidae			
Procyon lotor (Northern Raccoon)	1	Pers. Obs.	Appendix C
DIDELPHIMORPHIA			
Didelphidae			
Didelphis marsupialis (Common Opossum)	4	Camera trap	Appendix C
REPTILIA			
CROCODYLIA			
Crocodylidae			
Crocodylus acutus (American Crocodile)	3	Pers. Obs.	Appendix B
SQUAMATA			
Iguanidae			
Ctenosaura similis (Common Spiny-tailed Iguana)	2	Pers. Obs.	Appendix B
AVES			
ACCIPITRIFORMES			
Accipitridae			
Buteogallus subtilis (Mangrove Black-Hawk)	1	Pers. Obs.	Appendix D
FALCONIFORMES			
Falconidae			
Caracara cheriway (Crested Caracara)	2	Pers. Obs.	Appendix D
CATHARTIFORMES			
Cathartidae			
Coragyps atratus (American Black Vulture)	24	Camera trap	Appendix D
Cathartes aura (Turkey Vulture)	21	Camera trap	Appendix D
Sarcoramphus papa (King Vulture)	3	Pers. Obs.	Appendix D

Pers. Obs.: personal observations. Camera trap: recorded by camera traps located near the carcasses.

Relationship between vultures and carcass utilization by jaguars. Of the 24 predation events recorded during the study period, the jaguars dragged and hid 16 carcasses (66.6%) within the forest and eight carcasses (33.3%) within shrubland or beach vegetation. The jaguars dragged the sea turtles carcasses from the beach to the forest an average of 164.45 ± 219.48m (mean±SD, range = 1-678m). The jaguars fed on sea turtle carcasses an average of 1.47 days (1-5 days) and the average time that the vultures took to find and begin to eat from the sea turtle carcasses was 2.37 ± 1.83 days (1-7 days).

A positive and significant correlation was found between the number of days that the jaguars fed on the sea turtle carcasses (feeding-days) and the number of days that the vultures took to find and ate from the sea turtle carcasses (scavenging-days) ($r_s = 0.838$, $p < 0.001$; Table 2). A positive and significant correlation also existed between the feeding-days and the distance that the jaguar dragged the sea turtle carcasses from the beach to the forest (distance-beach) ($r_s = 0.781$, $p < 0.001$; Table 2). The feeding-days were negatively correlated with carapace length of sea turtles that were depredated by jaguars (turtle-length) but this correlation not was significant (Table 2).

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Table 2. Spearman Rank Multiple Correlation of the different variables related to sea turtle carcasses utilization by jaguars, at Nancite beach, Santa Rosa National Park, Costa Rica. The upper diagonal part contains correlation coefficient and lower diagonal part contains corresponding *p*-values.

	Feeding-days	Scavenging-(	Distance-beach	Turtle-length
Feeding-days	*****	0.838	0.781	-0.379
Scavenging-days	3.031e-07	*****	0.858	-0.249
Distance-beach	6.639e-06	7.855e-08	*****	-0.277
Turtle-length	0.067	0.239	0.189	*****

Feeding-days = number of days that the jaguars fed on the sea turtle carcasses. Scavenging-days = number of days that the vultures took to find and eat the sea turtle carcasses. Distance-beach = distance in meters that the jaguar dragged the sea turtle carcasses from the beach to the forest. Turtle-length = carapace length of sea turtles that were depredated by jaguars.

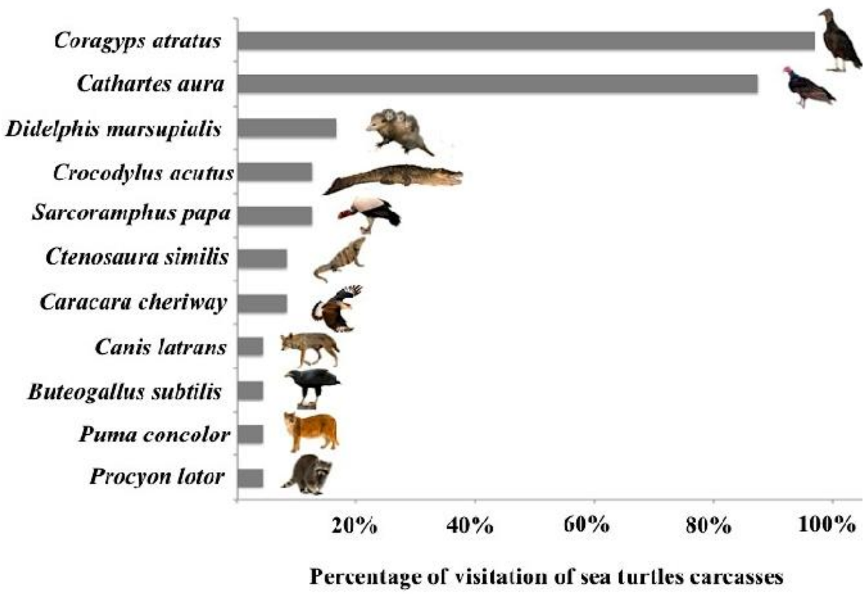

Fig. 3. Percentage of visitation of different vertebrate species that fed on sea turtle predated by jaguar (*Panthera onca*) at Nancite Beach, Santa Rosa National Park, Costa Rica.

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According to the linear models compared to evaluate feeding-days (see Table 3), this variable was best explained by scavenging days than by distance to the beach and turtle length. With every day that the vultures took to find and eat the sea turtle carcasses the jaguars fed 0.6 days more ($r^2 = 0.631$, p = 3.54e-06; Fig. 4). The scavenging-days were positive and significantly correlated with distance to the beach ($r_s = 0.858$, $p < 0.001$; Table 2). According to the linear model made to evaluate scavenging-days (see Table 3), this variable was best explained by distance to the beach. For every 100 m that the jaguar dragged the sea turtle carcasses from the beach to the forest, the vultures took 0.638 more days to find and eat the sea turtle carcasses (r^2 = 0.581, p = 1.5e-05; Fig. 4).

Table 3. Linear models used to evaluate the relations and effects of different variables on the consumption rate of sea turtles carcasses by jaguars (upper) and the days that the vultures took to find and eat the sea turtle carcasses (below), in Nancite Beach, Santa Rosa National Park, Costa Rica.

Linear Models	AICc	dAICc	df	Weight
Feeding-days ~ scavenging-days	69	0.0	3	0.4490
Feeding-days ~ scavenging-days + distance-beach	70.2	1.2	4	0.2417
Feeding-days ~ scavenging-days + vegetation	70.5	1.5	4	0.2115
Feeding-days ~ scavenging-days +distance-beach +vegetation	72.5	3.5	5	0.0772
Feeding-days ~ distance-beach	76.3	7.3	3	0.0117
Feeding-days ~ distance-beach + vegetation	76.9	7.9	4	0.0087
Feeding-days ~ vegetation	84.2	15.3	3	<0.001
Scavenging-days ~ distance-beach	82.6	0.0	3	0.518
Scavenging-days ~ distance-beach + vegetation	83.8	1.2	4	0.279
Scavenging-days ~ distance-beach + turtle-length	85.2	2.6	4	0.144
Scavenging-days ~ distance-beach + vegetation + turtle-length	87.0	4.4	5	0.057
Scavenging-days ~ vegetation	95.2	12.6	3	<0.001
Scavenging-days ~ vegetation + turtle-length	98	15.4	4	<0.001
Scavenging-days ~ turtle-length	103.2	20.6	3	<0.001

Feeding-days = number of days that the jaguars fed on the sea turtle carcasses. Scavenging-days = number of days that the vultures took to find and eat the carcasses. Distance-beach = distance in meters that the jaguar dragged carcasses from the beach to the forest. Vegetation = vegetation type (forest or scrub) where the jaguar hide the carcasses. Turtle-length = carapace length of sea turtles.

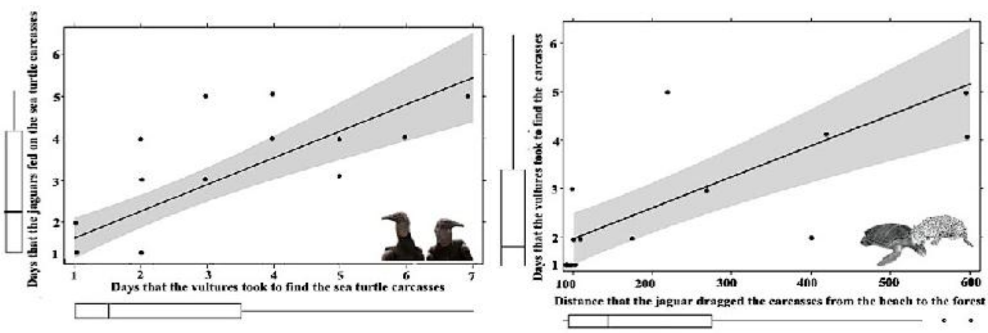

Fig. 4. Effect of the different variables recorded to the predation events by the jaguars (*Panthera onca*) on the sea turtles at Nancite Beach, Santa Rosa National Park, Costa Rica. Upper: Effect of the vulture activity on the consumption rate of sea turtles carcasses by jaguars. Below: Effect of the distance (m) that the jaguar dragged the sea turtle carcasses from the beach to the forest over the days that the vultures took to find and eat the carcasses.

Discussion

Scavengers of the sea turtle carcasses. Three major factors of vertebrate mortality make the sea turtle carcasses available to scavengers: (a) large predators, which subsidize scavengers with the remains of their kills, (b) natural deaths, and (c) mortality caused by human activity [6]. In most of the classical scientific manuscripts it is recognized that the large carnivores play an important role as top predators [26]. However, the importance of large carnivores as sponsors to scavengers has been poorly recognized in the classical literature, even when many researches have demonstrated the overwhelming importance of this [2, 6-8]. For the specific case of the jaguar, it is recognized as a top predator, as a flag and umbrella species and even some authors consider the jaguar as a keystone species [32-34]. Nevertheless, in most of the scientific literature, the importance of the jaguars as sponsors of scavengers has not been recognized [15]. Our results showed that many species of vertebrate scavengers are indirectly benefited by the predator-prey relationship between jaguars and sea turtles; in fact, eleven different vertebrate species were recorded scavenging at carcasses (see Table 1). This is an argument to recognize the ecological value of jaguars as top predators, flag, umbrella and keystone species that also provide carcasses to scavengers.

Many studies have demonstrated that in terrestrial habitats vertebrate scavengers are the main consumers of available carcasses [3, 6-7]. In our research, birds were the main scavenger group with five species recorded, followed by mammals with four species and in a lesser degree the reptiles with only two species. Birds are best specialized for carrion use because of the low cost of search efforts in soaring locomotion [35]. Soaring requires less energy than running [36], thus birds may search large areas more efficiently than mammalian or reptilian scavengers [37]. No mammals or reptiles have evolved into obligate scavengers, similarly within the bird's group, the old and new world vultures are the only known obligate terrestrial vertebrate scavengers [35, 37-38].

Of the 11 vertebrate species that we recorded scavenging on sea turtle carcasses, only five species (*Cathartes aura*, *Coragyps atratus*, *puma concolor, Sarcoramphus papa*, *Canis latrans*) had been recognized previously [15, 39-41]. The remaining six species had never been recorded scavenging at sea turtle carcasses [14-27]. Our observations also provided the first record of sea turtle in the diet of *Procyon lotor*, *Didelphis marsupialis*, *Crocodylus acutus*, *Ctenosaura similis*, *Buteogallus subtilis* and *Caracara cheriway*. The turkey vultures and black vultures were by far the main scavengers of sea turtles carcasses recorded in this work (see Fig. 3). The dominance of vultures in the use of carrion compared with other vertebrate scavengers had already been widely demonstrated in different works [42-44]. Turkey vultures consumed 90-95% of carcasses placed in a Panamanian forest [42], and in a similar study, vultures and mammalian scavengers located 63% and 5% of carcasses, respectively [43]. It has been postulated that the turkey vultures and black vultures outcompete other vertebrates by simply finding and consuming carrion more rapidly [42]. This is due to the supreme adaptations of new world vultures to a scavenging lifestyle, like their exceptional gliding ability [37] and an astonishing olfactory sense used to locate carrion [3].

Four ways whereby mammalian carnivores secure their food are: (a) Additive predation (i.e. killing healthy animals); (b) Compensatory predation (i.e. preying on young, old or sick animals vulnerable to mortality from other causes, thereby promoting the survival of the healthier of the prey population); (c) Kleptoparasitism (i.e. displacing other carnivores from their kills); (d) Scavenging (i.e. feeding only on animals that have died from disease, malnutrition, predation by another animal or other causes) [7]. We recorded the presence of large and medium carnivores such as cougars, raccoons, and coyotes feeding at sea turtle carcasses (see Appendix C**)**. These species besides scavengers might be behaving as kleptoparasites. By definition, kleptoparasitism (literally, parasitism by theft) is a form of feeding in which an animal takes preys or other food from the one that has caught, collected, or stored them [1, 7]. In mammalian carnivores, kleptoparasitism is generally performed by carnivores that displace directly other carnivores from their kills [3]. The case of kleptoparasitism presented in this work was unusual among mammalian carnivores because a direct displacement or combat did not occur between jaguar and other mammalian scavengers. This suggests competition by exploitation and not by interference. Further investigations are required to determine the true nature of the competitive interactions between kleptoparasites and jaguars.

A recent work highlighted that scavenging links have been underestimated in ecosystems ranging from marine to terrestrial, and that substantially more energy is transferred via scavenging links than via predation links [1]. Our case study is a good example of how the energy and nutrients flow from a marine ecosystem (through the bodies of sea turtles) to a terrestrial ecosystem (through the sea turtle predation by jaguars). Although in this case the predation was what facilitated the flow of energy and nutrients between sea and land, we believe that substantially more energy and nutrients are transferred by scavenging links (11 species benefited) than by the predation link (only one species benefited). The last published works on the trophic relationship between jaguars and sea turtles have highlighted the importance of this predatory interaction for the jaguars and the stability of terrestrial ecosystem, but indirect effects, including scavenging are widely underappreciated, poorly discussed and not highlighted. Further research is necessary to evaluate the importance of jaguars as providers of scavengers and facilitator of the flow of energy and nutrients between sea and land.

Relationship between vultures and carcass utilization by jaguars. After killing sea turtles on Nancite beach, jaguars dragged the carcasses into dense vegetation near to the beach in an attempt to conceal them from scavengers (see Fig. 3). The jaguars remained within the vicinity of the sea turtle carcass for up to five days, intermittently consuming the carcass over several nocturnal feeding bouts. The number of feeding bouts of the jaguars was correlated with the activity of vultures (see Fig. 4). If the vultures found the hidden turtle carcass in the morning after the night of the kill, the jaguars generally abandoned the carcass, consuming only a small portion of the sea turtle carcass. On the contrary, if the vultures took more days to find the hidden carcass, the jaguars generally returned for several nocturnal feeding bouts. This same ecological phenomenon has also been recorded with condors and pumas in Patagonia [45].

The interaction between large mammalian predators and vultures seems to be 'a complicated relationship of facilitation and competition'. The large mammalian predators can both facilitate scavengers by the remains of their prey, and compete with them by consuming these remains [3]. Factors like body size, sociality degree and food searching and consumption behavior of both large carnivores and scavengers can affect the direction and magnitude of the trophic interactions linking these two animal guilds [2-3, 6-7]. Carrion availability is partly mediated by both vultures and predators due to complex, density-dependent interactions across multiple trophic levels [2]. Thanks to the predatory activity of jaguars on sea turtles, the carcasses were available to at least the 11 scavengers recorded in this work. We found that jaguars both facilitated vultures by making carcasses available to them, and competed with them by continuing to eat from carcasses (see Fig. 4).

Some large felids consume the entirety of their prey within a few hours of the kill (e.g. lions) [46] leaving little available for vultures and therefore do not compete with them [2-3]. However, others large felids as leopards, cougars and jaguars usually consume small portions of the carcass over several days and therefore try to hide their prey from vultures and other predators (kleptoparasitism) [15, 47]. It has also been reported that vultures can outcompete mammalian carnivores [45, 49-50]. In ecology two fundamental types of competition (interference and exploitative) have been described [48]. Our results, following interference competition theory seem to favor large carnivores over vultures. Many researches have recorded that the presence of a large carnivore reduces the number of vultures at carcasses [35-38,42-50], and almost all top carnivores actively defend their kills from scavengers [6]. Nevertheless, the jaguars in our study area had a strictly nocturnal activity (personal observations) and on the other side the vultures have a strictly diurnal activity [42-44]. In the day, the jaguars were not present to defend their kills from vultures and other diurnal scavengers; this temporal segregation clearly favored the vultures. Therefore, for our case study, the vultures outcompeted the jaguars through exploitative rather than through interference competition. For example, we have observed that, once the vultures found a cadaver, they could consume the whole of it in one day.

In this work, we also found that the number of days the vultures took to find the sea turtle carcass was related with the distance that the jaguar dragged it from the beach to the forest (see Fig. 4). We believe that the more the carcass was dragged into the forest, the better hidden it was, and therefore the vultures took more time to find it. This same ecological phenomenon has also been recorded with condors and pumas in Patagonia [45]. Five decomposition stages of carrion have been identified: (1) recent death (fresh carcass), (2) early decomposition (discoloration), (3) advanced decomposition (first bone exposure), (4) skeletonization (drying of the bones) and (5) extreme decomposition (dry and weathered) [7]. The decomposition rate depends largely of the environmental conditions. The fresh stage is the time immediately following death when there is no odor, no discoloration, nor insect activity and, in general, it comprises six days after the death [7]. The turkey and black vultures are supremely adapted to a scavenging lifestyle and have an excellent sense of smell and vision [51]. However, during the first days after the depredation the turtle carcass is in the first stage of decomposition "fresh carcass", therefore it emits low odor and the vultures have to rely on sight to find it [7].

We documented that it was not important if the carcasses were well hidden into the forest, the vultures found them in a maximum of seven days. The carcasses of six days were in the second stage of decomposition presenting odor, swelling, discoloration and insect activity, and this facilitated the location of the carcasses by the vultures regardless of how well hidden they were. Our results suggested that vultures relied on sight during the first days to find turtle carcasses, which is why the carcasses that were more into the forest were the last to be found by vultures. As the decomposition of the carcass advanced, the vultures relied more on smell to find them, regardless of whether they were well hidden within the forest.

Conclusions and implications for conservation and management. To understand the basic ecological processes and the conservation importance of ecosystem elements that occur within an area that we wish to conserve and manage, is essential to make appropriate decisions that promote well-being and the permanence of wildlife. For example, the tropical dry forest of the Santa Rosa National Park presents a short rainy season with longer dry season [52]. According to climate change scenarios reported for Costa Rica, the area which comprises Santa Rosa National Park, will be much drier than it is now and it could possibly change from dry forest to xerophytic vegetation [53]. The dry seasons, climate change and the continuing events of "El Niño" phenomenon could change the distribution and abundance of the main prey of jaguars [53-54]. Sea turtles may be key resources for the jaguar in periods when the availability of other prey is low [22], as the nesting of sea turtles does not seem to be influenced by the dry seasons or rainfall [28-29], unlike the main prey of the jaguar inhabiting the dry forest of Santa Rosa: collared peccary and white-tailed deer, among others [55]. The scarcity of carrion within the ecosystems has detrimental effects on the behavior of scavengers as well as on the stability of ecosystems. Our results suggest that many species of vertebrate scavengers could be indirectly benefited by the predator-prey relationship between jaguars and sea turtles. Therefore, the sea turtles could be key resources for scavengers in periods when the availability of other types of carcasses is low.

Taking into account all the above arguments, efforts must be made to maintain the permanence of the trophic relationship between jaguars and sea turtles in the four major turtle nesting beaches of Santa Rosa, which requires management actions to mitigate all the threats that could disrupt this trophic relationship. For example, the Colorada, Nancite and Potrero Grande beaches have been fully protected from intrusive human activities, including tourism and support an intact wild ecosystem. However, in Naranjo beach, activities like tourism are allowed. Therefore, all the measures of management should be taken to avoid negative effects of the touristic activity on the important relationship between jaguars and sea turtles. The jaguar could be essential for the stability of the fauna in Santa Rosa by driving ecosystem processes, such as predation and scavenging, which can be heavily influenced by the ability of the jaguar to regulate and promote trophic interactions between sea and land. An important step in the conservation of jaguars and sea turtles is to integrate them into the management plan of Santa Rosa National Park. We fully recommend including jaguars and marine turtles as flagship species, since they are keystone species supporting ecosystem stability.

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Appendix A.

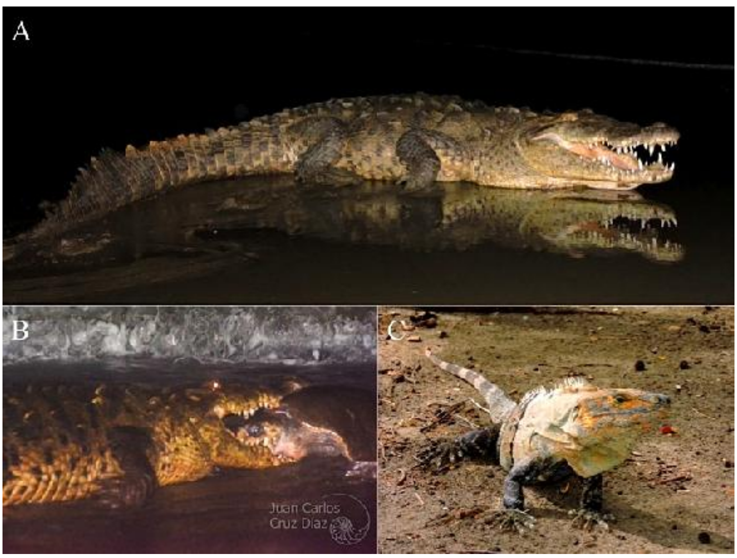
Data collected from the predation events of sea turtles by Jaguars (*Panthera onca*), at Nancite beach, Santa Rosa National Park, Costa Rica.

Predation events	Date	Feeding days	Scavenging days	Distance Beach (mts)	Vegetation type
1	5-Aug-2015	3	3	80	Forest
2	17-Aug-2015	2	1	10	Scrub
3	17-Aug-2015	1	1	4	Scrub
4	24-Aug-2015	3	2	400	Forest
5	26-Aug-2015	5	7	678	Forest
6	26-Aug-2015	2	1	12	Scrub
7	9-Sep-2015	4	2	105	Forest
8	17-Sep-2015	1	1	1	Scrub
9	1-Oct-2015	3	2	95	Forest
10	3-Oct-2015	2	1	7	Scrub
11	6-Oct-2015	4	4	431	Forest
12	6-Oct-2015	5	3	265	Forest
13	7-Oct-2015	1	1	18	Forest
14	11-Oct-2015	4	5	230	Forest
15	18-Oct-2015	1	1	2	Scrub
16	19-Oct-2015	1	1	18	Forest
17	20-Oct-2015	1	1	70	Forest
18	21-Oct-2015	1	1	3	Scrub
19	30-Oct-2015	3	5	634	Forest
20	4-Nov-2015	1	2	170	Forest
21	5-Nov-2015	1	1	9	Scrub
22	25-Nov-2015	2	1	22	Forest
23	30-Nov-2015	4	6	85	Forest
24	2-Dec-2015	5	4	598	Forest

Feeding days = number of days that the jaguars fed on the sea turtle carcasses. Scavenging days = number of days that the vultures took to find and eat the carcass. Distance beach = distance in meters that the jaguar dragged the carcass from the beach to the forest. Vegetation type = vegetation type (forest or scrub) where the jaguar hide the carcass.

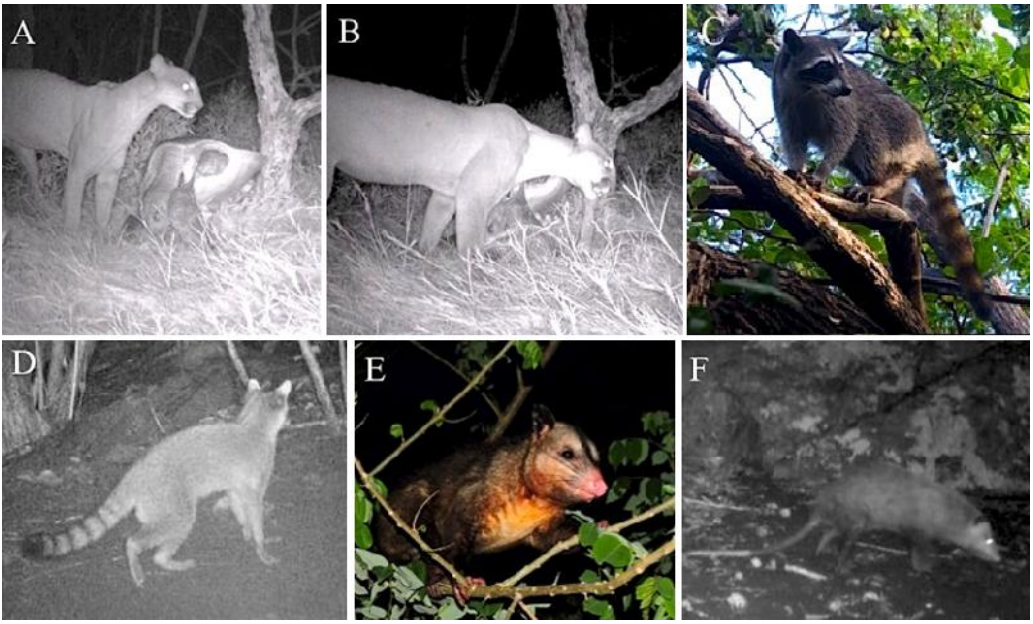
Appendix B.

Different reptiles species that scavenged over the sea turtle carcasses predated by jaguar, at Nancite beach, Costa Rica. (A-B) *Crocodylus acutus* (American Crocodile), (C) *Ctenosaura similis* (Common Spiny-tailed Iguana). Photos: (A and C) Sergio Escobar-Lasso, (B) Juan Carlos Cruz-Dias.



Appendix C.

Different mammalian species that scavenged over the sea turtle carcasses predated by jaguar, at Nancite beach, Costa Rica. Photos: Sergio Escobar-Lasso. (A-B) *Puma concolor* (Cougar), (C-D) *Procyon lotor* (Northern Raccoon), (E-F) *Didelphis marsupialis* (Common Opossum).



Appendix D.

Different avian species that scavenged over the sea turtle carcasses predated by jaguar, at Nancite beach, Costa Rica. (A) *Buteogallus subtilis* (Mangrove Black-Hawk), (B) *Caracara cheriway* (Crested Caracara), (C-D) *Coragyps atratus* (American Black Vulture), (E-F) *Cathartes aura* (Turkey Vulture), (G-H) *Sarcoramphus papa* (King Vulture). Photos: Sergio Escobar-Lasso.