Original Investigation

# Jaguars (*Panthera onca*) increase kill utilization rates and share prey in response to seasonal fluctuations in nesting green turtle (*Chelonia mydas mydas*) abundance in Tortuguero National Park, Costa Rica

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### ARTICLE INFO

### ABSTRACT

Jaguar (*Panthera onca*) predation of green turtles (*Chelonia mydas mydas*) is now a common occurrence in Tortuguero National Park, Costa Rica. The abundance of green turtles during nesting season ensures a constant provision of easy and predictable prey, however it is unknown to what extent jaguars consume turtle carcasses and how the jaguar population responds to limited turtle availability outside of nesting season. This study took advantage of the accessible nature of jaguar-predated turtle carcasses on Tortuguero Beach over a two year period (2011–2013), to provide a novel analysis of carcass utilization rates by jaguars and determine the effects of temporal fluctuations in green turtle nesting numbers. Camera traps were set-up on freshly predated turtles to capture jaguar activity across both Peak and Non Peak green turtle nesting seasons. Thirteen individual jaguars (five males, five females, three cubs) were captured returning to 77% of monitored turtle kills (60% Peak; 95% Non Peak). During Non Peak season, the number of jaguars per kill increased ($H(1) = 15.91$, $p < 0.001$) and total jaguar feeding time per kill also increased ($H(1) = 13.34$, $p < 0.001$). The propensity for *tolerated scavenging* or *sharing* during Non Peak season is illustrated by four adult jaguars captured interacting with a kill at separate times over two nights in October, 2012 (two males, two females). There were no significant differences between males and females, although there is a tendency for the latter to handle the prey to a greater extent. Although marine turtles may not to be a primary prey species, they play an important role in subsidizing the jaguars in this study. The increased kill utilization rates and prey sharing displayed by the jaguars, ensures optimal foraging during periods of low prey availability. These apparently atypical feeding behaviors may be unique to Tortuguero, however their prevalence across the jaguar's range should be considered.

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## Introduction

Jaguars (*Panthera onca*) are generally considered opportunistic feeders and are known to hunt a variety of different prey species across their range (Núñez et al., 2000; González and Miller, 2002; Scognamillo et al., 2003; Weckel et al., 2006; Cavalcanti and Gese, 2010). Terrestrial mammals generally constitute the predominant food items in the diets of jaguar populations (Núñez et al., 2000; Garla et al., 2001; Azevedo and Murray, 2007). In areas of low mammal availability, however, jaguars may be dependent upon abundant reptilian prey species, such as spectacled caiman (*Caiman crocodilus*) or freshwater chelonian species (Emmons, 1989; Azevedo and Murray, 2007; Cavalcanti and Gese, 2010; Da Silveira et al., 2010; Azevedo and Verdade, 2011).

After killing prey in an open area, jaguars will generally drag a carcass into dense vegetation in an attempt to conceal their kill from scavengers. Jaguars may then remain within the vicinity of the kill for up to three days, intermittently consuming a large proportion of the carcass over several feeding bouts. Jaguars may also abandon a carcass after the night of the kill, consuming only a small portion of the prey (Schaller and Vasconcelos, 1978; Schaller and Crawshaw,

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1980; Seymour, 1989; Jedrzejewski et al., 2014). Variations in felid kill utilization rates may be as a result of: prey availability, required search times, carcass spoilage rates and scavenging, or kleptoparasitism, by other vertebrates or conspecifics (Ogada et al., 2012; Elbroch and Wittmer, 2013; Elbroch et al., 2014; Ray et al., 2014)

Felid sociality is subject to significant variation and is contingent upon the availability and distribution of key resources (Sunquist and Sunquist, 1989). Jaguars may maintain exclusive ranges (Azevedo and Murray, 2007), however the majority of studies emphasize varying degrees of intrasexual and intersexual range overlap (Rabinowitz and Nottingham, 1986; Cavalcanti and Gese, 2009; Harmsen et al., 2009). Seasonal fluctuations in prey availability often trigger temporary alterations in individual jaguar ranging behavior and the exploitation of alternative prey species (Schaller and Crawshaw, 1980; Crawshaw and Quigley, 1991; Salom-Pérez et al., 2007; Carrillo et al., 2009; Cavalcanti and Gese, 2010). Although significant proportions of a jaguar's range can be shared with conspecifics, adult jaguars are firmly regarded as solitary hunters. Accounts of more than one jaguar feeding or scavenging from the same carcass are rare (Schaller and Crawshaw, 1980; González and Piña, 2002; Cavalcanti and Gese, 2009; Castañeda et al., 2013).

Tortuguero National Park (TNP) is considered the most important nesting ground in the western hemisphere for endangered green turtles (*Chelonia mydas mydas*) (Troëng and Rankin, 2005; IUCN, 2013). In the late 1990s, a steady increase in the number of jaguar-predated turtles, concurrent with an increase in the size of the green turtle rookery, was documented by The Sea Turtle Conservancy (STC). Since 2005, Global Vision International (GVI) has been carrying out surveys focused solely on this predator-prey relationship and the number of jaguar-predated turtles has continued to rise (Troëng, 2000; Troëng and Rankin, 2005; Veríssimo et al., 2012). Green turtles have constituted the majority of jaguar-predated turtles, however there have also been a small, but not insignificant, number of predated vulnerable leatherbacks (*Dermochelys coriacea)* and critically endangered hawksbills (*Eretmochelys imbricata*) (Veríssimo et al., 2012; IUCN 2013; GVI, unpublished results). Recent studies have now begun to focus on the ecology of Tortuguero's apex predator. It has been suggested that the jaguar predation of marine turtles was originally driven by reductions in the availability of primary prey species within TNP and an increase in anthropogenic pressures along the park's boundary (Troëng, 2000; Arroyo-Arce, 2013; Barca, 2013; Arroyo-Arce et al., 2014). Arroyo-Arce et al. (2014) identified sixteen individual adult jaguars present within the coastal habitat of TNP, with higher levels of jaguar occurrence associated with the seasonal presence of nesting green turtles.

Veríssimo et al. (2012) noted only partial consumption of jaguar-predated turtles. In addition, a significant proportion of kills were apparently discarded on the open beach during Peak green turtle nesting season. In contrast, outside of Peak nesting season, kills were predominantly found inside the coastal forest that immediately borders Tortuguero Beach (GVI, unpublished results). Incidental observations such as these, have highlighted the potential for temporal differences in how the jaguar population exploits a vulnerable prey and how these differences may be explained by dramatic fluctuations in the number of nesting green turtles. This study took advantage of the abundant and accessible nature of the marine turtle carcasses found on Tortuguero Beach, to provide the first description of turtle carcass utilization rates by jaguars and analyze whether green turtle availability influenced: (1) jaguar return rates to kills, (2) the total number of jaguars feeding from kills, (3) the total amount of time jaguars spend at kills and finally (4) if there were any differences between male and female kill utilization rates.
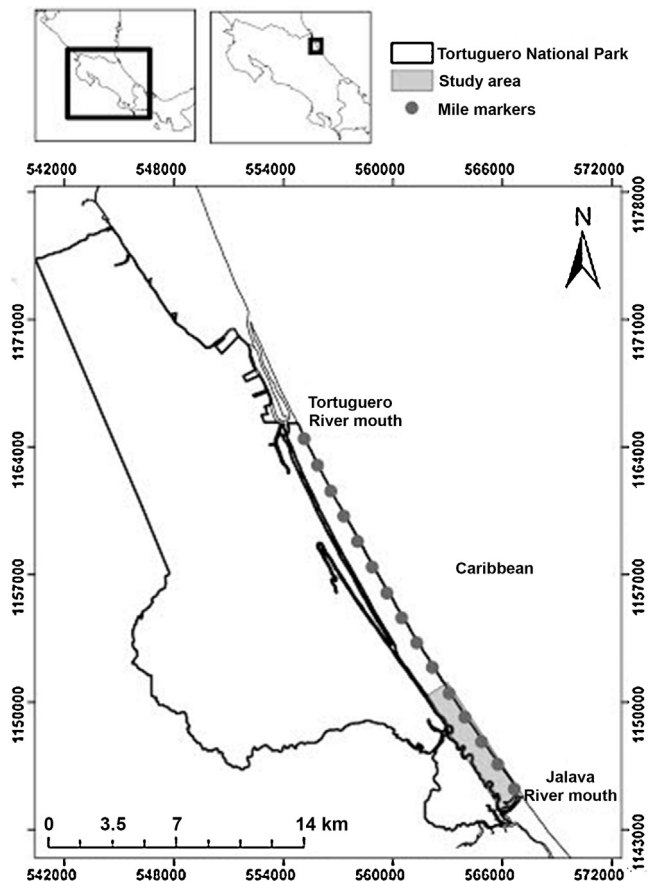


**Fig. 1.** Map of Tortuguero National Park, Costa Rica; Tortuguero Beach is demarcated into approximately 1600 m sections (denoted with circles) from kilometer 0 to kilometer 29. The study area is shaded (gray) on the southern end of the beach.

## Material and methods

### Study area

TNP is a 763 km$^2$ protected area on the North Caribbean coast of Costa Rica (10°32′28″N and 83°30′08″W) and incorporates both marine (502 km$^2$) and terrestrial zones (261 km$^2$) (Bermúdez and Hernández, 2004). Tortuguero Beach is 29 km in length, extending from Jalova River mouth in the south to Tortuguero River mouth in the north. Wet lowland tropical forest borders the entire beach with the exception of a coconut plantation and cattle ranch that extends from kilometer 28 to kilometer 27 in the south, and a combination of Tortuguero village, tourist lodges and an airport that extends from around kilometer zero to kilometer six in the north. This study focused on the 6 km of the southern section of beach (Fig. 1).

An average of 104,411 green turtle nests per year were recorded between the years of 1999 and 2003. This corresponds to a rookery size of 17,402–37,290 nesting females (Troëng and Rankin, 2005). Peak green turtle nesting season occurs from July until mid October with approximately 90% of all turtle nesting occasions occurring within this period. On any one night during Peak season, as many as 800 green turtles may nest on just the southern 5 km of the beach (Atkinson et al., 2011; Prieto and Harrison, 2012). Leatherback turtle nesting occurs predominantly from March through May with an annual estimation of 574 to 1623 leatherback nests (Troëng et al., 2004; Troëng et al., 2007). Hawksbill and endangered loggerhead (*Caretta caretta*) turtles (IUCN, 2013) nest occasionally, however there are no accurate estimations of their rookery sizes (Troëng, 1998, 2005; Prieto and Harrison, 2012). Approximately

1100 marine turtles were predated by jaguars between July 2005 and December 2013 (GVI, unpublished results).

### Data collection

Jaguar predation on marine turtles was assessed through morning beach surveys carried out between May 1st 2011 and May 15th 2013. Due to logistical constraints, only the 6 km on the southern extent of the beach could be surveyed. During these surveys, jaguar-predated turtles (hereafter known as kills) were recorded. On location of a kill, jaguar predation was assumed if jaguar tracks were found around the kill, characteristic puncture wounds were found on the kill's skull or neck, or the kill had been dragged. A kill was catalogued as a fresh kill (<24 h old) if there was: blood present, minimal amounts of flesh consumed (usually partial neck consumption), no putrid smell, little or no flies, no fly larvae and if the kill had not been previously documented. If a kill did not meet these criteria, it was not included in any analysis. The kill was recorded as either in the open (on the beach) or in the vegetation (in the forest or beach vegetation). Survey teams also searched the beach for any sign that indicated that a kill may be located inside the coastal forest. These signs included: turtle tracks that did not return to the sea, drag marks, and vulture activity. No kill was found further than 30 m into the coastal forest.

Camera traps (Bushnell Trophy 2010, 2011, 2011HD, 2012, and Moultrie Gamespy M80) were set-up either at the time of discovery of the kill or by an afternoon team on the same day. Cameras were set on either photograph or video (model dependent), and on a 30 s delay between successive photographs or videos. If the kill was in the vegetation, the camera was attached to a suitable tree, ideally around 3 m from the kill and 50 cm from the ground. If the kill was in the open, a tree was used if available and if not, a temporary post was set-up. Where possible, the kill was checked the following day, the memory card changed and the camera moved if the turtle had been dragged. On some occasions the kill was not revisited until after the second or third night. The camera was removed when either it was required to monitor another kill or all edible portions of the turtle were considered to have been consumed.

### Kill selection criteria

Only fresh kills were included in our analyses. Kills were also discarded from all analyses if there was suspected camera malfunction including: significant time gaps or suspected missed jaguar activity (e.g. no jaguars captured despite fresh jaguar tracks), or if the kill was dragged early in the night and an inaccurate depiction of jaguar activity had been recorded. Outside of Peak green turtle nesting season, the jaguars often dragged the kill away from cameras late on the first night or early on the second night. Due to these difficulties, only the first night of jaguar activity was suitable for statistical analysis. The first night was defined as from when the camera was set-up until 12:00 h the following day. Any information of relevance obtained from the second night or after is reported in a descriptive fashion.

### Data analysis

Individual jaguars were identified from the distinctive patterns of their coats (Silver et al., 2004) and referenced against a pre-existing jaguar database (GVI, unpublished results). All jaguars captured at kills were included in the analysis even if it was confirmed that they did not feed from the carcass. Feeding was ascertained when a jaguar was captured removing flesh or dragging the turtle.

Data were split into two seasons, Peak season (July 1st–October 15th) and Non Peak season (October 16th–June 30th), based on a combination of documented green turtle nesting trends (Atkinson et al. 2011; Prieto and Harrison 2012) and personal observations of significant changes in nesting frequency. Differences in the number of jaguars per kill, females per kill and males per kill between the seasons, were analyzed using the Kruskal–Wallis one-way analysis of variance. Difference in the number of males and females per kill for each season were tested using the Mann–Whitney $U$ test. To provide a relevant breakdown of the results, the same dataset was used to analyze several variables. Bonferroni correction was not considered necessary under the guidance of Nakagawa (2004).

To test whether there was a difference between the time jaguars spent at a kill between the seasons and therefore a difference in the amount of kill consumed, a smaller sample set was used. We included only kills that remained entirely in camera shot for the whole first night. The time jaguars spent at a kill for each occasion was calculated as the difference in time between the arrival of a jaguar and its departure as shown by the time stamp on the photographs or videos. We used a time of greater than 5 min to differentiate between separate jaguar occasions (e.g. if a jaguar was photographed twice at 23:34 and 23:38 it would be one occasion of 4 min. If a jaguar was photographed four times at 23:34 and 23:38, then again at 23:44 and 23:48, it would be two occasions of 4 min each and a total time spent at kill of 8 min). Total time spent at each kill was then calculated by combining the times of each jaguar occasion. If two jaguars were captured together at a kill at the same time, total time spent at kill was a combination of that of the individual jaguars (e.g. if males 1 and 2 were captured together at a kill for 20 min, total time spent at kill would be 40 min for that occasion). Differences in total jaguar time spent at kill, female time spent at kill and male time spent at kill between the seasons were tested using the Kruskal–Wallis one-way analysis of variance. The difference between male and female time spent at kill for each of the seasons were tested using the Mann–Whitney $U$ test. All statistical analyses were performed using Minitab 16 Statistical Software (2010, State College, PA, USA).

### Case study

At around 21:00 h on October 16th, 2012, a survey team followed a fresh turtle track from the high tide line to the vegetation. They discovered a recently predated green turtle (within the last few hours) dragged a few meters into the vegetation. To minimize interference, they left the kill without further inspection. At 10:00 h on October 17th, a team returned to the kill. The kill had canine puncture wounds to the neck but nothing else had been consumed, so a Bushnell Trophy 2011HD camera was then set on video and attached to a temporary post 2 m from the kill. The camera was collected three days later. A description of the captured footage is presented as an example of the general feeding and scavenging behavior displayed by jaguars interacting with a kill.

## Results

### Number of jaguars per kill

Our analysis included 39 kills (37 green turtles and two leatherbacks) surveyed for the first night after the kill, with a total of 890 camera trapping hours (mean ± SD = 22.82 ± 3.24); 20 kills for Peak season (all green turtles) (451 camera trapping hours mean ± SD = 22.54 ± 2.98) and 19 kills for Non Peak season (17 green turtles and two leatherbacks) (439 camera trapping hours mean ± SD = 23.12 ± 2.98).

A total of 13 different jaguars were captured visiting kills on the first night: five males (M), five females (F) and three cubs (C) (Fig. 2). We captured jaguar activity at 12 out of the 20 kills (60%
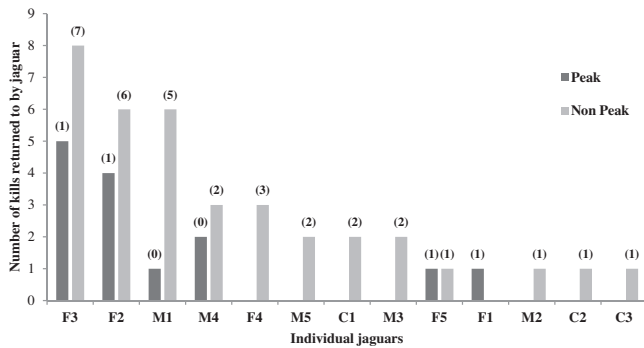
**Fig. 2.** Individual jaguars (*Panthera onca*) and the total number of kills returned to by each jaguar, captured using camera traps on the night after the kill, during both Peak and Non Peak green turtle (*Chelonia mydas mydas*) nesting seasons in Tortuguero National Park, Costa Rica, 2011–2013 (Peak *n* = 20, Non Peak *n* = 19). In parentheses: total number of kills each jaguar was captured 'scavenging from' or 'sharing with' at least one other jaguar.

return rate) monitored during Peak season (Fig. 3). Out of the 12 Peak season kills with captured jaguar activity, we confirmed that no feeding occurred at four kills. These four kills were visited briefly by a single individual. During Non Peak season, we captured jaguar activity at 18 out of the 19 kills monitored (95% return rate) (Fig. 3). We captured two or more jaguars at 14 out of the 19 kills monitored during Non Peak season. This meant that in these 14 cases, one or more jaguars were either 'scavenging from' or 'sharing with' another jaguar and its kill. This scavenging or sharing behavior was more prevalent during Non Peak season than Peak season, as significantly more jaguars were captured per kill ($H(1) = 15.91$, $p < 0.001$) (Fig. 4a). At seven out of the 18 kills with captured jaguar activity during Non Peak season, two jaguars were captured sharing a kill at the same time: M1/M4, M1/F2, M1/F5, M5/F4, M3/F1 and F2/C1 (captured together at two kills). F3 and her two cubs, C2 and C3, were captured together at one kill.

During Peak season, no jaguar activity was captured at any kill monitored after the first night (*n* = 14). During Non Peak season, we recorded jaguar activity on the second night at eight kills (*n* = 16) and recorded jaguar activity on the third night, or later, at six kills (*n* = 10).

During Non Peak season, we captured more females per kill ($H(1) = 4.08$, $p < 0.05$) and more males per kill ($H(1) = 5.11$, $p < 0.05$) than during Peak season (Fig. 4b and c). We also captured more females per kill (Peak mean ± SD = 0.50 ± 0.61; Non Peak mean ± SD = 0.95 ± 0.71) than males per kill (Peak mean ± SD = 0.20 ± 0.41; Non Peak mean ± SD = 0.68 ± 0.75) during
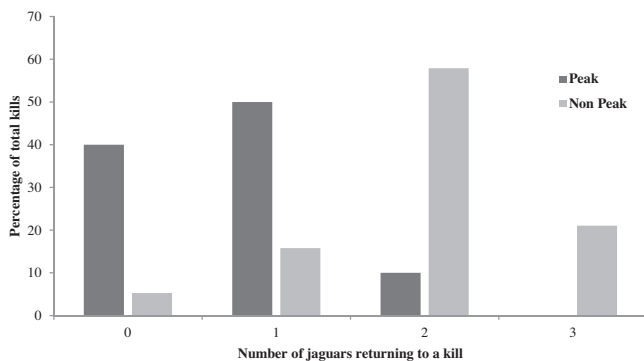


**Fig. 3.** Jaguar return rate: percentage of the total number of kills that were returned to by a total of 0, 1, 2, or 3 individual jaguars (*Panthera onca*), captured using camera traps on the night after the kill, during both Peak and Non Peak green turtle (*Chelonia mydas mydas*) nesting seasons in Tortuguero National Park, Costa Rica, 2011–2013 (Peak *n* = 20, Non Peak *n* = 19).
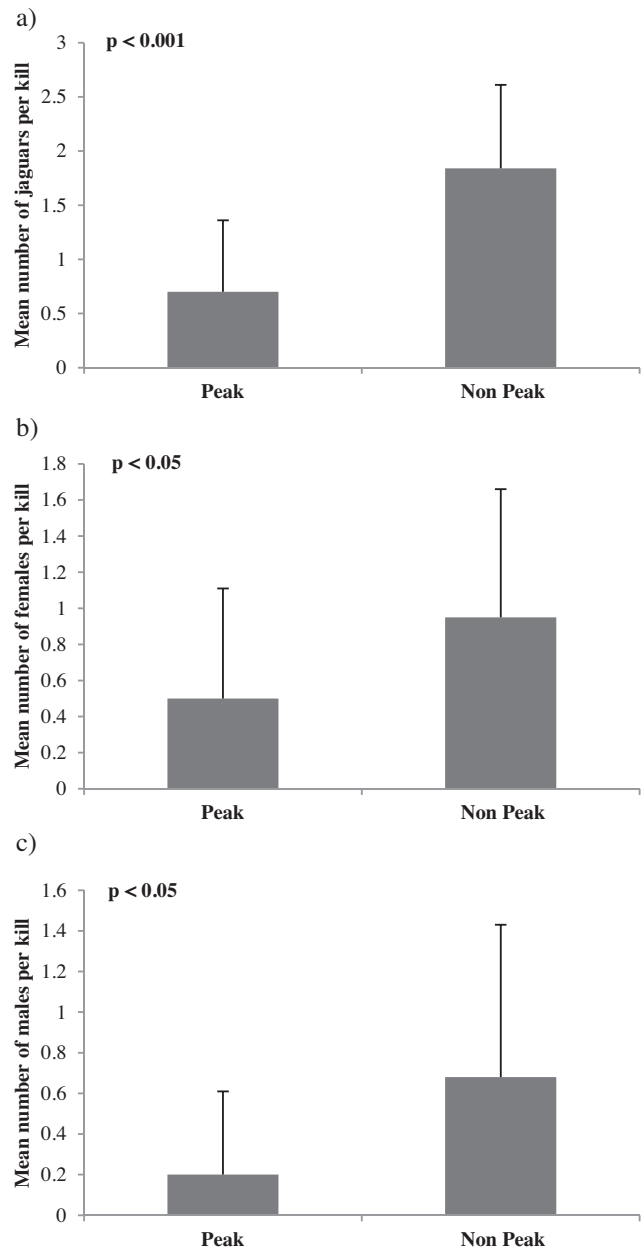


**Fig. 4.** Effects of green turtle (*Chelonia mydas mydas*) nesting season on the number of jaguars (*Panthera onca*) captured per kill: (a) mean number of jaguars captured per kill (b) mean number of female jaguars captured per kill (c) mean number of male jaguars captured per kill, in Tortuguero National Park, Costa Rica, 2011–2013 (Peak *n* = 20, Non-Peak *n* = 19).

both Peak and Non Peak season, however the differences between the number of males and females captured were not significant (Peak $W(1) = 462$, $p = 0.088$; Non Peak $W(1) = 407.5$, $p = 0.249$).

*Time spent at kill*

Twenty two kills were regarded as suitable for the analysis of time spent at kill. Eight kills were monitored during Non Peak season (six green turtles, two leatherbacks) (181 camera trapping hours; mean ± SD = 22.66 ± 3.27) and 14 kills were monitored during Peak season (all green turtles) (311 camera trapping hours; mean ± SD = 22.23 ± 3.11).

We confirmed that jaguars spent more time at kills on the first night during Non Peak season than Peak season ($H(1) = 13.34$,
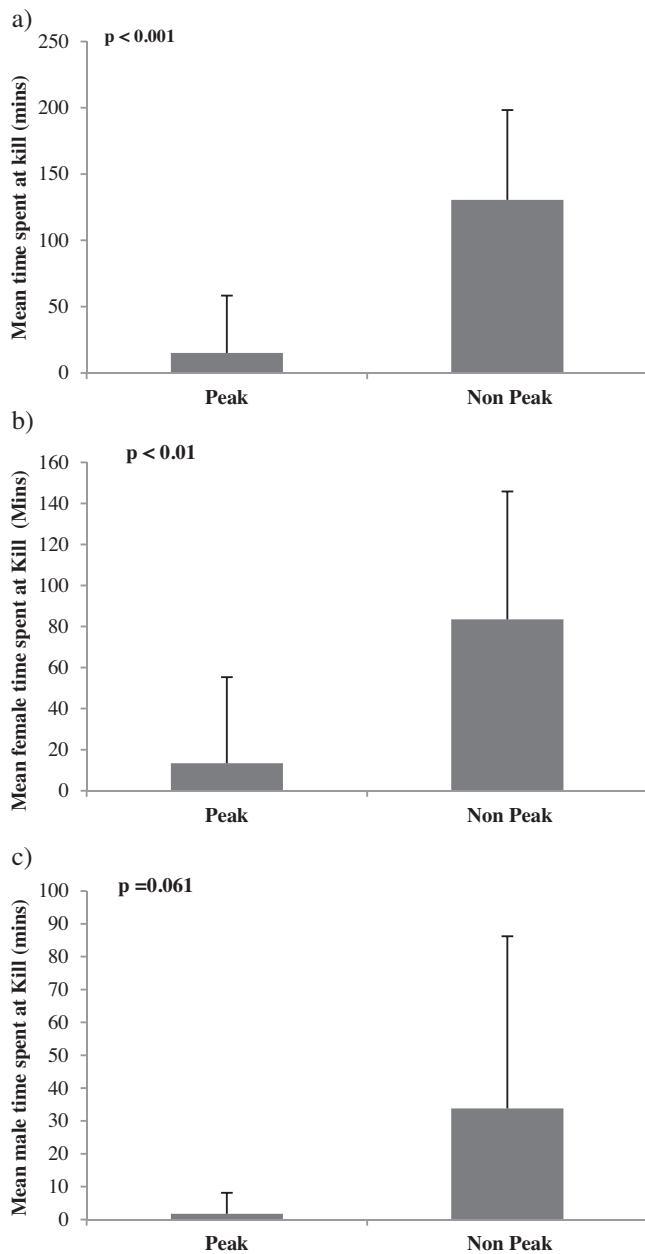
**Fig. 5.** Effects of green turtle (*Chelonia mydas mydas*) nesting season on the overall time jaguars (*Panthera onca*) spent at each kill: (a) mean jaguar time spent at each kill (min) (b) mean female jaguar time spent at each kill (min) and (c) mean male jaguar time spent at each kill (min), in Tortuguero National Park, Costa Rica, 2011–2013 (Peak $n$ = 14, Non Peak $n$ = 8).

**Table 1**
Date and time individual jaguars (*Panthera onca*) were captured interacting with a green turtle (*Chelonia mydas mydas*) kill, time jaguars spent at kill and behavior documented, with a camera trap in Tortuguero National Park, Costa Rica on October 17th–19th, 2012.

| Date | Hour | Jaguar | Minutes | Behavior |
|---|---|---|---|---|
| 17 Oct | 20:19 | F3 | 31 | Feeding |
| 17 Oct | 21:53 | F3 | 29 | Feeding |
| 17 Oct | 22:25 | F2 | 14 | Feeding |
| 17 Oct | 22:45 | F2 | 4 | Feeding |
| 18 Oct | 01:54 | F2 | 16 | Feeding |
| 18 Oct | 02:17 | F2 | 1 | Passing by |
| 18 Oct | 03:45 | F3 | 4 | Feeding |
| 18 Oct | 05:26 | F3 | 17 | Feeding |
| 18 Oct | 18:36 | F3 | 6 | Feeding |
| 18 Oct | 19:34 | M4 | 2 | Sniffing kill |
| 18 Oct | 19:37 | M1 | 1 | Sniffing vegetation |
| 18 Oct | 19:38 | M4 | 6 | Feeding/dragging kill |
| 19 Oct | 01:45 | F2 | 2 | Sniffing vegetation |

$W(1) = 211$, $p = 0.094$; Non Peak $W(1) = 84$, $p = 0.261$). We captured M5 spending 124 min (11 occasions) at a kill in March 2013, and M1 and M4 spent a combined time of 107 min at a leatherback kill in February 2013. The maximum time we documented a female spending at a kill was 122 min by F3 (5 occasions) in November 2012.

*Case study*

No black vulture (*Coragyps atratus*) activity was recorded on October 17th, 2012, prior to the first night of automatic recording. A time series of jaguar occasions is detailed in Table 1 and this kill involved the four jaguars captured most frequently during this study (Fig. 2). Three of the jaguars were confirmed to feed from the kill and therefore at least two of them were considered to be 'scavenging from' or 'sharing with' another jaguar and its kill. F2 and F3 initially displayed similar feeding behaviors. The females crouched down at the kill's right shoulder and tore flesh from the neck. The skin between the carapace and plastron was then torn away to allow access to the muscles and viscera. The jaguars continued feeding on the internals using either the *scooping* technique (Fig. 6a) or by forcing their snouts into the wound (Fig. 6b). The *scooping* technique involves inserting an inverted front paw into the carcass and then licking the spoils from the foot pad. F2 was captured eviscerating the carcass and subsequently chewing on the intestinal tract on two occasions. F2 was also recorded carrying away parts of the kill toward the forest. She was captured with different male companions on several occasions in 2012 (e.g. Fig. 6c) and eventually, was recorded on a coastal forest trail accompanied by a cub on October 20th, 2012 (GVI, unpublished results), suggesting that she may have been going to feed the cub somewhere nearby. Between 07:05 and 14:25 h on October 18th, there was extensive black vulture activity; predominantly feeding from the jaguar created wounds. F3 spent a short time early on the second night, continuing to feed from the carcass. M4 briefly investigated the carcass and immediately after, M1 spent only a minute sniffing the vegetation without any carcass interaction. Shortly after, M4 was captured chewing at the flippers prior to dragging the kill toward the forest (Fig. 6d) and out of camera shot. When the cameras were picked up, the carcass was located 15 m further into the vegetation.

**Discussion**

This study has shown that marine turtles constitute a dietary component for a large number of jaguars in Tortuguero and that individual jaguars will utilize this prey more than was originally believed. Over the study period, the overall jaguar return rate was

$p < 0.001$) (Fig. 5a). In fact, we recorded significant feeding at only two out of the 14 kills we monitored during Peak season. At the first of these two kills, we captured M3 and F1, sub-adults at the time of capture, spending a combined total of 56 min at a kill in July 2011. At the second kill, F2 and F3 were captured spending a combined total of 156 min at a kill in July 2012.

Females and males spent more time at kills during Non Peak season than during Peak season, however this difference was not significant for males (females: $H(1) = 9.86$, $p < 0.01$; males: $H(1) = 3.52$, $p = 0.061$) (Fig. 5b and c). On average, females (Peak mean ± SD = 13.4 ± 41.9; Non Peak mean ± SD = 83.5 ± 52.4) spent more time at kills than males (Peak mean ± SD = 1.71 ± 6.41; Non Peak mean ± SD = 33.8 ± 52.4) during both Peak and Non Peak seasons, however these differences were not significant (Peak

**Fig. 6.** Camera trap photos of jaguar (*Panthera onca*) feeding on marine turtles in Tortuguero National Park, Costa Rica; (a) F2 *scooping* from a green turtle (*Chelonia mydas mydas*) on June 10th, 2012 (b) F3 *inserting* her snout between the green turtle carapace and plastron on July 30th, 2012 (c) M1 and F2 *sharing* a green turtle on June 11th, 2012 (d) M4 *dragging* green turtle on October 18th, 2012. Photo credit: GVI Costa Rica.

77% on the first night after the kill. Núñez et al. (2000) reported just a 50% return rate to prey carcasses in Jalisco, Mexico. Differences in jaguar return rates between periods of high and low prey availability were also suggested by Núñez et al. (2000). Our results demonstrate that the seasonal decrease in nesting green turtles triggers a significant increase in the amount of time jaguars spend intermittently consuming a kill. Previous reports of partial consumption therefore do not accurately reflect kill utilization rates by jaguars (Troëng, 2000; Veríssimo et al., 2012). During Peak season, jaguars will rarely patrol more than a few hundred meters of beach before locating a nesting turtle. However, during Non Peak season, they may need to search for several kilometers over several nights before finding a nesting turtle or another jaguar's kill. Extensive search times will require jaguars to optimize foraging and consume considerably more during Non Peak season. The number of predated turtles is significantly greater during Peak season (Veríssimo et al., 2012), but kills are often abandoned without concealment and generally only partial consumption occurs on the night of the kill. A fresh kill provides the advantage of *choice* tissue selection, a behavior utilized by black bears *Ursus americanus* predating salmon *Oncorhynchus* spp. (Reimchen, 2000). Further investigations are required to determine the effects that black vulture or invertebrate scavenging may have on jaguar return rates or handling times. Initial evidence suggests that black vulture abundance is greater during Peak season and avian scavengers have been shown to reduce both the overall number of felids and time spent by felids at kills (Ogada et al., 2012; Elbroch and Wittmer, 2013). Increased invertebrate activity and spoilage rates can be considered as increased kill competition, and may also reduce kill utilization rates (Elbroch et al., 2014; Ray et al., 2014).

Facultative scavenging is common amongst vertebrates (DeVault et al., 2003; Selva et al., 2005) and is a behavior that has been documented in the largely sympatric puma (*Puma concolor*; Ross and Jalkotzy, 1996; Bauer et al., 2005; Bacon and Boyce, 2010). Literature evidence of jaguars scavenging, particularly from another jaguar's kill, is scarce and usually involves prey that have died from causes other than predation (González and Piña,

2002; Cavalcanti and Gese, 2010; Castañeda et al., 2013). Camera traps have been employed to document a male and female jaguar scavenging from an adult cow (*Bos taurus)* carcass (González and Piña, 2002), and two males scavenging from a marine dolphin (Delphinidae) carcass (Castañeda et al., 2013). Obvious limitations in our methodology prevented identification of the individual responsible for each kill. However, as all the jaguars were captured feeding at multiple jaguar kills, it is accurate to assume that most of the jaguars recorded in this study are *facultative scavengers* and will regularly share another jaguar's kill. Ubiquitous scavenging during Non Peak season is in response to the resource pulse provided by a kill at a time when prey availability (i.e. nesting marine turtles) is low (Castañeda et al., 2013; Fallows et al., 2013). The number of occasions jaguars were captured sharing kills coupled with the close proximity in time different jaguars were often captured at a kill (as highlighted in the case study), suggest this is *tolerated scavenging* or a *sharing deal* as opposed to kleptoparasitism. There was no evidence to suggest that this scavenging may have a significant impact on the kill utilization rates or predation rates of an individual jaguar; effects that have been described with interspecific scavenging such as the black bear kleptoparasitism of puma kills (Elbroch et al., 2014). The ample amount of turtle meat provides more than enough food to satiate an individual jaguar over one night. The loss of energetic benefits from allowing another jaguar to share a kill is minimal in comparison to the risk of injury from another individual in a densely populated food patch (Arroyo-Arce et al., 2014), where jaguar home ranges are likely to have been established in response to aggregations of a seasonally predictable and vulnerable prey, as has been reported in Corcovado National Park (Salom-Pérez et al., 2007).

The variations in kill exploitation between males and females may be explained by sexual or individual differentiation in prey preference (Cavalcanti and Gese, 2010). It could also be a reflection on the small size of the study area and that male jaguars generally occupy larger home ranges. Both M1 and M4 have been captured on the coastal trails along the northern section of the beach (Arroyo-Arce, 2013), and it is probable that they regularly

predate turtles along the entire stretch of Tortuguero Beach. The importance of abundant, large vulnerable prey for females that are pregnant or with dependent young has been suggested in pumas (Ross and Jalkotzy, 1996; Jansen and Jenks, 2012). Jedrzejewski et al. (2014) have also reported that, by killing a calf every night, a female jaguar would secure the constant provision of food for both herself and her cub. Both F2 and F3 were seen with cubs, in October 2012 and May 2013, respectively, and their almost exclusive utilization of monitored kills in the Peak season of 2012 may be part of their own strategy to ensure a continual food supply. Recently independent sub-adults could also heavily rely on learned hunting or scavenging behaviors, even during Peak season, as may have been the case with M3 and F1 in July, 2011.

## Conclusions

This study has revealed that a reduction in marine turtle availability will increase overall kill utilization rates by jaguars and more specifically; (1) the rate at which jaguars return to a kill, (2) the number of jaguars that will 'scavenge from' or 'share' a kill and (3) the amount of time a jaguar will spend consuming a kill. The potential for differences between male and female kill utilization rates has also been postulated.

Our results have revealed higher levels of kill consumption than previously reported and an apparently high level of social tolerance that merits further investigation. The described *tolerated scavenging* or *sharing deal* may just be a strategy to optimize foraging in response to low levels of prey availability. However, we believe that future genetic studies could elucidate interesting information on the relatedness of Tortuguero's individuals and may indicate the potential existence of a jaguar family group, centered around residents (M1, M4, F2 and F3) identified during a long term coastal forest monitoring program (GVI, unpublished results).

The recorded behaviors could be also the result of a locally learned behavior, passed down several generations, which have now become prevalent across the jaguars living in the area. However, the potential for facultative scavenging or food sharing being common behaviors across the jaguar's range, should also be considered. This may be particularly relevant when investigating jaguar/livestock conflicts as individuals considered responsible for depredation events may have simply been taking advantage of an easy meal.

The low availability of alternative prey species within TNP as a result of illegal hunting is likely to have played a pivotal role in the initial development of the jaguar-turtle relationship (Arroyo-Arce, 2013; Arroyo-Arce et al., 2014). Even though there have been notable increases in predation rates, the importance of marine turtles in the diets of jaguars remains undetermined. With only 1100 turtles predated between 2005 and 2013, the dense jaguar population of TNP is not solely dependent on turtles. Further studies are still required to elucidate what constitutes the remainder of the jaguar diets and where jaguars focus their foraging efforts outside of green nesting turtle season.

## Conflict of interest statement

Authors Guilder, Barca and Gramajo were all previously employed as field scientists by GVI Costa Rica. Stephanny Arroyo-Arce is an independent researcher. Roberto Salom-Pérez is the country director for the Panthera Costa Rica Program and regional director for the Mesoamerica program. We consider there to be no conflicts of interest and all aspects of this study were developed by the authors on behalf of their respective organizations.

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