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Short communication

Surplus killing of olive ridley (*Lepidochelys olivace*) by jaguar (*Panthera onca)* in Santa Rosa National Park, Costa Rica

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ABSTRACT

Surplus killing is a rare behavior in large predators and its documentation has been scarce. This phenomenon has been observed mostly in carnivores and comprises on the predation of several prey in a short period that eventually would not be consumed, this behavior presents a challenge to ecological theory because it appears to be a waste of energy. Although there are several records of surplus killing behavior for the *Panthera* genus, this behavior has not been reported on free roaming jaguar (*Panthera onca*) populations. Hence, this report describes in-situ evidence of surplus killing by jaguars during the arribada massive nesting on olive ridleys (*Lepidochelys olivacea*) in Nancite beach, Santa Rosa National Park, Costa Rica. This new report has interesting implications for food web theory, as it shows that under certain circumstances some predators are capable of killing more prey than they can consume, showing how strong the hunting instinct can be for certain species.

The surplus killing behavior was first described for carnivores in 1972 (Kruuk, 1972). This behavior is a predatory response in which an individual predator will kill more prey than it needs to satisfy its hunger, during the same hunt and without consuming all of the kills (Lucherini et al., 2018). Surplus killing should not be confused with other multiple killing events such as parallel killing, where a predator hunted additional prey in which it still consumes the carcass of a prey from its previous hunt (Duľa and Krofel, 2020). Therefore, the surplus killing behavior in wild carnivore populations might represent a waste of energy, due there is free access to the carcass and it is not used, and thus exhibiting an energy expense without the energy reward (Kruuk, 1972). Evidence suggest that this behavior arises from a strong hunting instinct present in carnivores as an evolutionary trait by facilitating the capture of available prey whenever there is an opportunity (Oksanen et al., 1985). As a result, surplus killing behavior is so strong that it can even lead the predator to hunt, overcoming the feeling of need or satiety (Kruuk, 1972).

The species where this behavior has been reported are varied (Kruuk, 1972), it exhibits a functional response in which the predatory instinc arises to an unusual increase in the prey availability. As a result, this behavior contradicts the typical satiety found in predadors (Linell et al., 1999) and makes these events rare in nature, since they can only occur under specific conditions (Zimmermann et al., 2015).

Such specific conditions for a surplus killing event to occur must be a favorable combination of environmental and geographical conditions (Zimmermann et al., 2015), in addition to an abundant number of prey that exceds the limit capacity to repel an eventual predator attack (Delgiudice, 1998), being described in nature only for a few number of predators (Kruuk, 1972) i.e., pygmy owl (*Glaucidium passerinum*) (Solheim, 1984); killer whales (*Orcinus orca*) (Gaydos et al., 2014); weasels (*Mustela frenata, Mustela nivalis*) (Jedrzejewska and Jedrzejewski, 1989) and stoats (*Mustela ermine*) (Oksanen et al., 1985). Surplus killing is most commonly described in felines, canines and ursids. In canines surplus killing have been reported in red foxes (*Vulpes vulpes*), dingos (*Canis lupus dingo*) and wolves (*Canis lupus*) (Delgiudice, 1998). Meanwhile, in feline species, this behavior has been observed in pumas (*Puma concolor*) preying on flocks of domestic animals (calves, sheep, goats and pigs), caracals (*Caracal caracal*) (Stuart, 1986; Lucherini et al., 2018), leopards (*Panthera pardus*), snow leopards *(Panthera uncia)* (Stuart, 1986), and lions (*Panthera leo*) on cattle, horses and gnous (*Connochaetes gnou*) (Kruuk, 1972), but despite the fact that this behavior has been reported in different species of the *Phantera* genus, to date there is no record of

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Fig. 1. Sequence of predation of olive ridley (*Lepidochelis olivacea*) by a jaguar (*Panthera onca*) recorded in a documentary (Dohrn, 2019). The follow sequence showed a jaguar individual preying on a first sea turtle(A), when a second turtle catches its attention (B), leaves the first sea turtle killed intact (C), and goes to kill the second (D).

Fig. 2. Olive ridley (*Lepidochelis olivacea*) arribada in Nancite beach during the surplus killing event. Note the multiple sea turtles during nesting activity at the same time (photograph taken with an infrared night vision monocular).

reports in jaguars.

Currently, there is no field evidence of surplus killing for jaguars, thus this note presents two independent field observations of different jaguar individuals killing multiple olive ridleys *(Lepidochelys olivcea)* during a single predation event. Both observations occurred during massive nesting of olive ridleys, called “arribadas” (≥1000 turtles nesting simultaneously) (Cornelius and Robinson, 1982) in Nancite beach (10° 48'13.32"N 85 41'53.97"W), Santa Rosa National Park, Costa Rica.

The first surplus killing observation occurred in November 2017 during the recording of the documentary "The Secret Life of Jaguars"(Dohrn, 2019), where a sequence of predation of two olive ridleys was recorded when both individuals came ashore and the same jaguar individual killed both turtles, the entire event was recorded in one continuous shot where the predator was never lost sight of. During this event an adult jaguar was observed approaching a nesting turtle, the jaguar killed the turtle with a bite on the turtle's neck, but did not consume it. However, a few minutes later the jaguar abandoned the first carcass and prey on a second individual 50 m away from the first turtle leaving the first individual dead without consuming any of its meat (Fig. 1)(Dohrn, 2019). During the night of the event, it was not recorded that the jaguar returned to consume the first turtle; it only partially consumed the second turtle, in the part of the neck and the first third of the carcass.

The second observation of a jaguar surplus killing occurred in September 21, 2019 during nocturnal surveys of arribada nesting of olive ridley (Fig. 2). The observation took place at the southern section of Nancite beach, while using a long-range infrared night vision scope (Bushnell Equinox Night vision 4.5x40 monocular). We were able to observe an adult male jaguar walking on the beach approximately 100m from our position. The jaguar approached an olive ridley that was nesting nearby, and the jaguar proceeded to bite and remove the top portion of the ridley skull, then began to lick the blood that flowed from it, the jaguar only licked the blood that came out of the bite with which it killed the turtle, but did not consume any of the turtle's meat. Ultimately, the jaguar dragged the turtle carcass to the vegetation line, it has been described that jaguars usually hunt turtles on the beach, drag them to the vegetation line and eat them inside the forest (Alfaro et al., 2016). Minutes later, when the jaguar was dragging the turtle up to the line of vegetation, this same jaguar individual looked in the direction of another turtle, which was nesting 4 meters from its last position. The

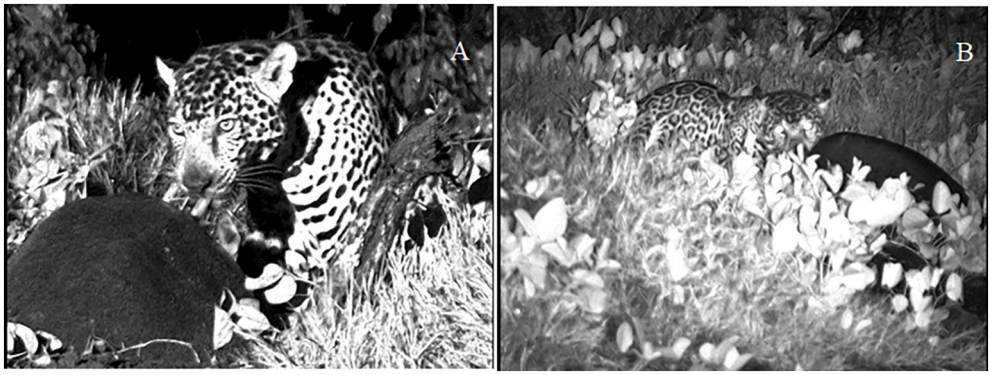

Fig. 3. A jaguar individual eating an olive ridley (*Lepidochelis olivacea*) during a second killing event (A). Jaguar dragged the olive ridley carcass into the forest to feed it. (Photograph taken with an infrared night vision monocular).

Fig. 4. Evidence of another olive ridley ridley (*Lepidochelis olivacea*) preyed by a jaguar the morning after the surplus killing event. The carcass showed the deep wound injuries caused by the jaguar canines when it was killed, but it was not consumed.

jaguar abandoned the first olive ridley, and began to approach the other nesting sea turtle and killed it in the same manner as the previous turtle. The jaguar dragged the second turtle carcass towards the vegetation line into the bushes. The jaguar consumed the second turtle for approximately 30 minutes, it consumed approximately 40% of the turtle's meat, he broke the shell near the neck to gain access to the inside of the turtle, it consumed some viscera, he was able to extract them using his arm, this predatory behavior is similar to that described by other researchers for jaguars when they consume turtles (Alfaro et al., 2016). After which it proceeded to drag the carcass of the second turtle further into the forest (Fig. 3) meanwhile leaving the first turtle without consuming it, only with the wound in the neck with which he killed it, but without consuming any of its meat.

When we returned the next morning to the predation site, we found the first olive ridley carcass with no signs of having been consumed, a second partially consumed carcass three meters away (Fig. 4) and a third olive ridley carcass with pattern of neck wound as the first turtle, and likewise without signs of consumption. This means in total we found the 2 turtles that we witnessed when the same jaguar killed them, and one more that was probably hunted after we made the observation, with no signs of consumption. Although we did not confirm that the third olive ridley predation was attributable to the same jaguar individual, we can assumed due the closeness of the three carcasses (three meters away from the second carcass), that it did not appear that the predation on the three olive ridley carcass during consecutive days that we monitor.

Sea turtle predation by jaguars has been well documented for several decades (Carrillo et al., 1994), and due the slowness during nesting, sea turtles become vulnerable and predictable prey to opportunistic predators such as the jaguar (Montalvo et al., 2020). Even though there are eight beaches in the world where arribadas of olive ridley occur (Cornelius and Robinson, 1982), none have reported insights of surplus killing behavior of opportunistic predators such the jaguar. We speculate that the spatiotemporal overlap and availability of a large number of prey with limited mobility and without the ability to repel an eventual attack has led to the surplus killing in jaguars as has been described for other carnivore species (Kruuk, 1972).

The surplus behavior, as documented in these observations, continues to be a conundrum which goes against the optimal forage theory (MacArthur and Pianka, 1966) where predators tend to maximize their resources by utilizing the lowest amount of energy (Caraco et al., 1980). As possible explanation to this behavior,we hypothesized that this is a survival instinct strategy in which predators kill opportunistically abundant prey; as well as allowing the use of carcasses to other conspecifics within their group i.e. females with cubs killing multiple prey consecutively, young individuals during training or inexperienced individuals (Kruuk, 1972). As alternative theories to surplus killing as an explanation for this behavior, it is possible that the human presence could have disturbed the predator and because this reason the jaguar abandoned the first turtle, but it is worth mentioning that in both cases a distance of approximately 100 m from the event was maintained and the jaguar showed no sign of significant disturbance, as it proceeded to feed on the next turtle it hunted for a considerable period of time. Another

alternative theory is that the jaguar has killed a surplus with the intention of returning in the next few days to feed on these prey (Lucherini et al., 2018) this theory could be better adjusted to optimal foraging (Caraco et al., 1980), but we do not observe any evidence that the jaguar has returned in the following days to consume the carcass.

Although in energetic terms surplus killing is inconsistent, the hypothesis holds that this small disadvantage given by the strong hunting instinct which encourages carnivores to kill whenever there is an opportunity, even in isolated and rare events in which it wastes energy; it is a small disadvantage compared to the great survival advantage that a predator obtains by having a very strong hunting instinct that will be useful in most cases for its survival (Oksanen et al., 1985). On the contrary, Delgiudice (1998) describes surplus killing as a disadvantage from killing several prey over a short period, which in turn causes a waste in energy as a result of stress. Owing to our observations, we support the hypothesis of survival instinct strategy which is only reinforced by the marked resource scarcity in a seasonal ecosystems such as the dry tropical forest, availability of vulnerable prey such sea turtle arribadas represents an important opportunity for jaguars, therefore losing the sense of whether stop or continuing hunting. Nesting beaches in Santa Rosa National Park are unique places for jaguar nursery and gathering (Montalvo et al., 2020), thus our observations of surplus killing during the peaks olive ridley nesting season is feasible. Finally, for such behavior we speculated sea turtles have not development adaptative strategies to avoid terrestrial predators such jaguars (Carrillo et al., 1994). Thus, massive sea turtle arribadas could trigger the surplus killing in jaguars, suggesting females with offspring, young individuals in training and adult males can invest a low energy budget during surplus killing as an useful instinct that guarantees survival during scarcity periods in seasonal ecosystems such the tropical dry forest.

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Declaration of Competing Interest

None.

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