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A biomechanical model to assess the injury risk of leopards (*Panthera pardus*) hunting by free falling from trees

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Abstract

Leopards have been observed to ambush prey by jumping down on it from trees. There are both anecdotal reports and video recordings of this hunting behavior. Here we conducted a biomechanical analysis of this technique to assess the degree of risk for the predator in such cases. We concluded that the risk of suffering severe injuries seems to be too high for this technique to be a usual way of predation on horned mammals such as male impalas. Our results can be useful in discussing proposed paleobiological hunting scenarios and living predators' strategies of managing risks.

Keywords: *Panthera pardus*, hunting risk, free-falling, hunting behavior, predator-prey interactions

Introduction

Leopards (*Panthera pardus*) hunt chiefly by stalking prey or by ambush, during which the animal uses the advantages of its covered habitat. The leopard may make a short, extraordinarily fast dash at its victim from the stalk or ambush position. It kills smaller prey by biting the nape of the neck or puncturing the skull with its canines, whereas larger prey is bitten on the throat, allowing the leopard to avoid the horns and antlers of antelope and deer (Kruuk and Turner, 1967; Bothma and Le Riche, 1984; Bothma and Le Riche, 1989; Bothma, Van Rooyen and Le Riche, 1997; Stander, Haden, Kaqece and Ghau, 1997; Turner, 1997; Sunquist and Sunquist, 2002; Bailey, 2005; Jenny and Zuberbühler, 2005; Balme, Hunter and Slotow, 2007; Stein and Haysen, 2013). Additionally, there is evidence of leopards using flexible hunting strategy (Bothma and Le Riche, 1989), prey-specific hunting tactics (Bothma, Van Rooyen and Le Riche, 1997), and differences in the hunting behavior of forest leopards from that of savannah leopards (Jenny and Zuberbühler, 2005). Attempts only ended in kills in 5 % of hunts in the Serengeti (Bertram, 1982), 16 % of hunts in the Kruger (Bailey, 2005), and 38 % of hunts in Kaudom, Namibia (Stander, Haden, Kaqece and Ghau, 1997). Furthermore, between 5 % and 10 % of kills are lost to other predators, especially lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) (Bailey, 2005). Leopards minimize kleptoparasitism by caching carcasses in trees, caves, and large burrows or by dragging them into dense vegetation (Sunquist and Sunquist, 2002).

There are some uses of trees for hunting behavior discussed in the literature (Kruuk and Turner, 1967; Hart, Katenbo and Punga, 1996; Sunquist and Sunquist, 2002 and references therein). Some species of primates are hunted in trees by leopards (Sunquist and Sunquist, 2002 and references therein). Leopards of the Ituri Forest in Zaire were observed patrolling fruiting trees known to be visited by duikers and bush pigs. Carcasses of prey were found in the vicinity of these trees as well (Hart, Katenbo and Punga, 1996). In the Serengeti area, twice a leopard was seen resting on a high branch of a tree when it perceived a reedbuck near the

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dense shrubbery below. It then came down the trunk, crept very slowly towards the reedbuck, and when it was very near, jumped at it, missing on one occasion (Kruuk and Turner, 1967).

There has not been much discussion of hunting by free falling from trees, which has been documented in some videos (Leopard — Cheetah Channel 2017, Kruger Sightings 2019, ACID 2018, Shock wave 2019, Shazal 2015) and anecdotally reported (Hunter, 1952). A well-studied analog is the diving hunting behavior of predatory birds. Sometimes falcons go to high altitudes and then descend from those heights, using gravity to increase their speed. Maximum hunt speeds in a dive are largely variable based on the duration of the dive, acceleration before the dive, and the steepness of the dive, but values greater than 100 km/h have been recorded (Hart, Wreford, Brown and Downs, 2018). *Falco peregrinus* may exceed 200 km/h (Tucker, Cade and Tucker, 1998; Hart, Wreford, Brown and Downs, 2018).

Falcons presumably approach prey at a speed that balances the risk of injuring themselves against the risk of failing to catch prey; this should favor lower speeds than the maximum theoretically available in a dive (Tucker, Cade and Tucker, 1998; Tucker, 1998). Although the falcon's speed is much higher than that of leopards, the birds can control their speed in a dive by changing their drag and choosing the length of the dive (Tucker, 1998). Compared to falcons, the aerodynamic forces on the free-falling leopards are very small, since there is not much control of the speed and direction after losing contact with the tree (Vogel, 2009). This behavior seems highly risky due to accidental collisions at high speed and without many possibilities of making adjustments to the speed and direction. Therefore, it is expected that this behavior occurs only sporadically.

In leopards, free-falling over prey such as male impalas implies an injury risk due to a misplaced collision of the leopard's chest or head against the impala's back or horns. Injuries have been relatively well studied in raptors and carnivores and can be fairly common (Mukherjee and Heithaus, 2013). Dislocation of joints (Ackermann and Redig, 1997) and broken toes, talons, flight feathers, and injured eyes are widely documented in raptors (Mukherjee and Heithaus, 2013). In Canada, 5.9 % of American kestrels had hunting-related injuries (Murza, Bortolotti and Dawson, 2000), 14 % of 98 individuals of raptors in northern Arkansas had injuries (Bedrosian and Pierre, 2007). Inspection of museum specimens of Accipiter hawks revealed that 18.6 % of 339 individuals had hunting injuries (Roth, Jones and French, 2002). High rates of fractured canines were recorded for some species of the order Carnivora. For representatives of the genus *Panthera,* the values are 5.4 % for lions (*Panthera leo*), 9.2 % for tigers (*Panthera tigris*), and 9.8 % for leopards (*Panthera pardus*) (Table 3 in Van Valkenburgh,

2009). The observed breakage rates are likely to be due to injuries sustained by moving and struggling prey during hunting (Van Valkenburgh and Hertel, 1993). Few data are available for the proportion of individuals injured by prey in soft tissues or other parts of the body. Such injuries are known to occur; for example, African wild dogs may incur deep cuts, broken teeth, and injured limbs (Creel and Creel, 2002).

It has been highlighted that it will be a challenge to quantify the risks of injury in the wild. The collection of such data in situations where there are changes in prey availability that might affect willingness to take risks or invasions of potentially dangerous prey should be an important avenue of future research for behavioral ecologists (Mukherjee and Heithaus, 2013). The study of skeletal-injury frequency and distribution is an interesting clue for paleobiological inferences of hunting behavior in predatory vertebrates (Brown, Balisi, Shaw and Van Valkenburgh, 2017; Van Valkenburgh, 2009; Van Valkenburgh and Hertel, 1993). Moreover, the biomechanical evaluation of injury risks derived from hunting behaviors is useful for discussing paleobiological hunting scenarios (Farlow, Smith and Robinson, 1995; Krauss and Robinson, 2013).

Here we applied a biomechanical model (Sturdivan, Viano and Champion, 2004; Frank et al., 2011) to assess the leopard's risk of injury while performing free-falling hunting. Similar approaches were already attempted in paleontological studies of predator–prey interaction (Krauss and Robinson, 2013). We also discussed some implications of our results for the general understanding of predator's risk of injury management and paleobiological inferences.

Material and methods

Collision analysis

In the analyzed situation, an inelastic collision is observed in a hunting situation where a leopard jumps from a tree and hits an impala. The leopard carries the initial mechanical energy in kinetic form during the fall. This energy is partially transmitted on impact, modifying the kinetic energy of both animals. An amount of this initial energy is dispersed in the form of sounds, heat, and mainly dangerous deformations of biological tissues for both specimens. This released energy will be called Q, and it is of vital importance when evaluating risks or possible damage to both prey and predator. Considering that the initial speed of the impala is zero, the following expression is reached for the energy released in the shock:

$$Q = K_i \left(1 - \left(\frac{e^2 + v}{1 + v} \right) \right), \qquad (1)$$

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where e is the coefficient of restitution, K_i is the initial kinetic energy of the free-falling leopard, and v is the ratio of the masses m of the leopard and M of the impala ($v = m/M$). For the case of interest, where the leopard falls clinging to its prey, the shock can be modeled as a perfectly inelastic collision, and equation (1) will transform into:

$$Q = K_i \left(\frac{1}{1+v} \right). \qquad (2)$$

This energy is a fraction of the initial one and will be available, to a greater extent, to cause damage to the biological tissues involved, as long as the leopard directly impacts the impala. However, this does not usually happen since the leopard has a significant amount of muscle mass in its strong forelimbs with which it absorbs part of the energy. This capacity of muscle to absorb energy during forced stretching is estimated by using the following equation:

$$\sigma \cdot \varepsilon = \frac{F}{A} \cdot \frac{\Delta l}{l} = \frac{W}{V}, \qquad (3)$$

where l is the muscle length, Δl is the length variation of the muscle, A is the muscle cross-section area, V is the muscle volume, and W is the work involved in forced stretching of the muscle. The maximum stress of rat leg muscles measured experimentally is close to $\sigma = 300$ kPa, and the maximum deformation is around $\varepsilon = 0.25$ (Alexander, 2003). Equation (3) predicts an energy absorption capacity of 75 J per kilogram of muscle mass. All these are typical values for vertebrate striated muscle (Alexander, 2003 and references therein). The main muscle groups that the leopard comprises by absorbing energy from its fall on the impala are the pectorals, triceps, manus extensors, and deltoids. In the literature, there is no precise data about the mass of these muscles in *P. pardus*, so the information available from a different species of similar body mass (*Panthera uncia*) was used instead, which is considered the best available approximation (Cuff et al., 2016). The snow leopard (*P. uncia*) is different in hunting strategy and body proportions (including forelimb weight) to the leopard (*P. pardus*); therefore, the inaccuracies derived from this approximation were tackled by performing a sensitivity analysis with considerable variations (33 %) on the mass of the muscles. The muscles in each leg involved in absorbing energy from its fall add 1.490 kg of muscle mass for a female *P. uncia* of 36 kg (Cuff et al., 2016). Assuming a similar value for *P. pardus*, we estimated that it could absorb 112 J of energy with its front legs before impacting with its chest on the loin of the prey, as the studied videos show. This implies that the following equation gives the energy available to cause damage:

$$Q_{ef} = Q - 112 \text{ J.} \qquad (4)$$

After the contact of forelegs against the impala, the leopard continues falling and strikes the impala's body with the chest or head. We modeled these kinds of collisions between the chest or head of the leopard against the back or head of the impala. The energy available was assumed as in equation (4).

Data analysis

Five videos showing leopards hunting impalas by free falling from trees were collected (Leopard — Cheetah Channel 2017, Kruger Sightings 2019, ACID 2018, Shock wave 2019, Shazal 2015) and analyzed with the software Tracker 5.1.5 (Open Source Physics). The objects were manually tracked due to poor automatic discernment between objects and background. The tip of the snout of the leopard was chosen as the point of mass. To estimate the scale, we used the average body length of a leopard in two cases (Leopard — Cheetah Channel 2017, Kruger Sightings 2019) and the average shoulder height of an impala in the other three (ACID 2018, Shock wave 2019, Shazal 2015). The average shoulder height is 86.1 cm for impala, and the average body mass is 48.75 kg (Frey et al., 2019). For a female leopard, the average body and head length is 106.5 cm (Stein and Hayssen, 2013). We took this value, corresponding to a female because we have accurate data of the mass of forelimb muscles for a female specimen of *P. uncia* with a body mass of 36 kg (Cuff et al., 2016). The typical body mass values for female *P. pardus* are consistent with this value (Stein and Hayssen, 2013).

From the videos, all the height values from which the predator falls were rather similar (Appendix 1), with variations within the errors due to the uncertainties in the scale choice. For that reason, we preferred to use the average height value of 3.55 m and consider the variations and uncertainties in a sensitivity analysis. Therefore, the typical distance of free-falling before the collision was considered as 2.69 m. The initial vertical speed is negligible in all cases. Hence, the initial mechanical energy is equal to the gravitational potential energy of the leopard. Therefore, considering the initial height of the leopard's center of mass minus the impala's height at shoulder, and using the data of the masses, the value of Q given by equation (2) is 545.7 J. Accordingly, equation (4) provides that $Q_{ef} = 433.9$ J. There would be a second impact, from the impala's shoulder height to the ground, where the leopard could also use the hindlimbs to absorb the residual kinetic energy. This fall would probably not suppose a much greater risk to the leopard, and it was neglected in our analysis.

Injury risk assessment using the Blunt Criterion modified (BCm)

The Blunt Criterion parameter (Sturdivan, Viano and Champion, 2004) used to predict injury risk is defined by the following equation:

$$BC = \ln\left(\frac{E}{m^{(1/3)}TD}\right), \qquad (5)$$

where $m^{1/3}$ is the cubic root of the mass of the struck body, with the mass in kilograms, E is the kinetic energy of the projectile in meters per seconds, T is the thickness of the body wall at the impact location on the individual, and D is the diameter, in centimeters, for the impact area. The numerator in equation (5) represents the energy available to cause damage. The previously estimated energy Q_{ef} is a good estimation for E (Sturdivan, Viano and Champion, 2004). The denominator is a semiempirical expression of the animal's capacity to absorb and tolerate the energy of the impact. In this case, the evaluation of damage focuses on the leopard, who also contributed the initial kinetic energy. So, the BC criterion adapted for our case is:

$$BC_m = \ln\left(\frac{Q_{ef}}{m^{(1/3)}TD}\right). \qquad (6)$$

The chest wall thickness of predator (T) was estimated based on the method of Sturdivan, Viano and Champion (2004), where $T = k.m^{1/3}$. We choose 0.789 for the parameter k: the value for dogs and the highest of the values available (Table 1 in Sturdivan, Viano and Champion, 2004).

The injury risks were assessed in four situations that range from a normal hunting situation to an extremely risky one. We considered the four combinations of the leopard's chest or head colliding accidentally against the back or the horn of the impala. The trauma of a forelimb would also be highly disadvantageous for survival. Therefore, the analysis for a forelimb would be interesting (both against the body and a horn). However, the methods used here were developed, refined, and experimentally tested only for chest and head collisions (Sturdivan, Viano and Champion, 2004; Frank et al., 2011). For general discussion, we assumed that forelimbs are biomechanically better suited to support collisions than the chest or head because the limbs are adapted for supporting high loads during jumping or running. It is highly likely that the risk evaluation of forelimbs injuries would be smaller than the other cases, and even if that is not the case, forelimbs injuries would not involve death in the short term.

The following values were used for calculating the modified Blunt Criterion: for collisions against a horn you must use only the mass of the head of the impala as

M. It was estimated as $M = 8.4$ kg by using a rough estimation of the volume from scaled images and considering a mean density of 1,000 kg/m³. The estimated thickness of the soft tissue of the leopard's chest was $T = 2.61$ cm. The diameters of the impact area (D) against the back of the impala were estimated considering the chest's dimensions and the head of an average leopard from scaled photos. For a collision with the leopard chest against the back of the impala, the diameter was estimated as $D = 32.7$ cm, and for a collision with the head of the leopard against the back of the impala, $D = 16.0$ cm. For the leopard head, we considered a mass m = 3.1 kg and a T value of 1.15 cm. For collisions against the horn, we made the following considerations: When a small, blunt object hits the body, the area of contact is just the cross-sectional area of the projectile. As the projectile size increases, the area of contact is determined by the curvature of the projectile and the body part struck. The effective diameter was calculated as the deformed surface of the skin by a cone of radius 0.4 cm (the diameter of the tip of impala's horn) and height equal to the distance T that must penetrate before producing serious damage. These measurements were taken from images of a male impala's head scaled on software Tracker 5.1.5 (Open Source Physics). Therefore, for collisions against a horn, the obtained effective diameter value of $D = 2.1$ cm was considered.

Probability of lethality and AIS scale

The probability of lethal blunt trauma due to non-penetrating impact is given according to a multiparametric lethality model to estimate the probability of a non-penetrating projectile causing lethal blunt trauma to the thorax. This model was based upon a compilation of empirical databases derived from live-animal tests (Sturdivan, Viano and Champion, 2004). The equation presented in the international metric system (MKS) is the following (Frank et al. 2011):

$$P_L = \frac{1}{1 + e^{\left(39.9192 - 3.597 \cdot \ln\left(\frac{Q_{ef}}{m^{(1/3)}TD}\right)\right)}}. \qquad (7)$$

The results are compared using the 1985 AIS scale (see Sturdivan, Viano and Champion, 2004; Frank et al., 2011; and references therein). The value of AIS corresponding to BC_m values was obtained by a linear fit of the data presented in Sturdivan, Viano and Champion (2004).

To estimate errors due to uncertainties in the measurements and estimations of the model parameters we made, a sensitivity analysis was done, considering extreme variations in linear dimensions of 10 %. That

Table 1. Results of the biomechanical model

Situation	BC Value	Probability of lethal blunt trauma, %	AIS estimated Value
Leopard chest — Impala body	0.43 (−0.62–0.97)	0.53 (0.1–3.5)	2.6 (0.0–3.9)
Leopard chest — Horn	2.32 (2.15–2.72)	82.5 (72.0–95.3)	7.3 (6.9–8.3)
Leopard head — Impala body	1.05 (0.62–1.45)	4.71 (1.0–17,3)	4.1 (3.1–5.1)
Leopard head — Horn	3.66 (3.13–4.07)	99.8 (98.9–99.9)	10.6 (9.3–11.7)

The errors estimated by the sensitivity analysis are shown between parenthesis.

implies extreme variations of 21 % in areas and 33 % in masses.

Results

The main results are shown in Table 1. The probability of lethal blunt trauma seems to be relatively high even in the most usual situation of the leopard chest colliding against the impala body (0.1–3.5 %). In the case of an impact against a horn, it is almost certainly a fatal result (see Table 1). All this suggests that high accuracy in leopard movements is required to avoid lethal injuries, and this technique must be used only exceptionally. The leopard's average speed at the collision, after free-falling from 2.69 m height, is slightly larger than 7 m/s (see Appendix 1 for detailed measurements for each video). The sensitivity analysis provided an estimated error in the results that are displayed in Table 1.

Discussion

From simple physics considerations and the measurements from video tracking (see Methods section and Appendix 1), we concluded that the time of the leopard's free-falling before collision is roughly 0.7 s. If the impala's reaction time is around 0.1 or 0.2 s and the acceleration is close to 7 m/s² (Alexander, 2003), the time required to evade the collision is larger than the time available. Thus, free-falling hunting seems to be highly successful if the prey does not detect the stalking leopard in advance. However, the estimated risk of injury during free falling hunting, between 0.1 % and 3.5 % in one of the better situations (see Table 1), seems too high for a predator like a leopard that must hunt at least once a week for several years (Schaller, 1972). The high associated risk may explain why this behavior has been only occasionally recorded, and that it is highly unusual in leopards and other large felids. Moreover, this behavior requires the ability to choose the right moment to initiate the free-falling. To miss the target would imply losing the prey, and falling over the horns would imply an extremely high risk of lethal injury. If we consider our biomechanical model, a collision between animals of similar body size produces the same probability of damage for both. In the case of a successful collision against the trunk of the impala, it is unlikely that the leopard produces lethal damage. Therefore, this hunting behavior seems to be suitable for bringing down or catching the prey, but the probability that the collision itself produces significant damage when hunting prey of similar size is very low (3.5 % at most). This observation is consistent with the fact that there is no video where the impala seems to be lethally injured only by the collision. The recorded free-falling hunting probably is only an unusual opportunistic behavior in leopards.

Another interesting observation is that the measured collision speed of around 7 m/s is smaller than the maximum running speed of a charging leopard (Alexander, 2003). Therefore, the high risk involved in free-falling hunting is mostly due to the lack of control, but not due to the high collision speed. Crucial points seem to be the choice of prey and the timing of free falling to avoid a collision with horns. In three of the analyzed videos, the prey were females or juveniles (ACID 2018, Shock wave 2019, Shazal 2015), which would indicate that the leopards prefer to avoid the possible damage caused by the horns of the male impala, making this hunting strategy safer. Although, presumably under pressure from scarcity conditions or opportunism, attacks on males were also observed in two of the analyzed videos (Leopard — Cheetah Channel 2017, Kruger Sightings 2019). Moreover, the two attacks on horned males seem to be from a lower height than all the others. In one of those hunts (Kruger Sightings, 2019), the leopard slightly changed its direction by pushing its limbs against the tree. When attacking horned prey, leopards are probably more cautious and prefer lower heights and increased control to reduce the risks. The low variation in height probably results from a tradeoff between being undetected and maintaining a low value of the injury risk. Leopards seem to have difficulties handling free falls from a height larger than 4 or 5 meters since no heights above this level were observed in the studied videos. However, due to the small number of videos analyzed, all our suggestions about impala sex and age preferences and prevalence conclusions are highly speculative, and further observations are needed to test these issues.

The methods proposed here can be useful to study some paleobiological scenarios involving collisions between predators and prey or during intraspecific fighting. For example, it was proposed that pachycephalosaurs' domed skulls were adaptations for head butting behavior (Galton, 1971). However, the hypothesis of agonistic head-to-head butting was considered questionable because the small contact area of opposing heads would produce serious injuries (Alexander, 1989). Instead, flank-butting was suggested based on the analogy with extant African antelopes, and it was suggested that this kind of behavior would produce pain in the opponent without causing serious injuries (Carpenter 1997). The methods presented here could be helpful to compare both hypotheses. For *Tyrannosaurus rex* a hunting scenario was proposed involving collisions with heavy prey such as *Triceratops* (Krauss and Robinson, 2013) that can be evaluated in depth by using the methods to determine lethal blunt trauma. The Miocene sabretooth borhyaenoid *Thylacosmilus atrox* (Riggs, 1934; Goin and Pascual, 1987) also presents as a unique feature a domed skull, formed by the enlarged maxillary bones that house the upper canines (Janis et al., 2020). The maxillae of *T. atrox* are extensively pitted and grooved in all specimens, suggestive of some particular soft tissue covering (Janis et al., 2020), and a corneous covering was proposed (Riggs, 1934). These and other anatomical features could lead to the highly speculative hypothesis that *T. atrox* used head butting against prey or conspecifics (Francisco Goin, personal communication, May 18th, 1996). The head-butting hypothesis can be tested considering the risk of injuries of such behavior. Traumatic injuries directed to the neck, chest, and back (compression of vertebrae, compression stress fractures of limb bones, and dislocations) in *Smilodon* suggest violent and powerful contact with heavy prey (Turner, 1997). This can indicate an ambush hunting type, with short pursuit and violent impact with prey before the fatal slash (Argot, 2004 and references therein). This is another example where our methods would be helpful to determine the likelihood of different scenarios.

Not only can our general methods be useful for paleobiological studies, but also our results on free-fall hunting. The risk of free-falling hunting is too high to be used frequently by a predator. Any slight misalignment during the fall would produce a probability of lethal blunt trauma close to 2 % and, in some cases, much larger (see Table 1). Therefore any adaptation to change body orientation during free fall would increase the chances of success. In the case of leopards, the tail is probably very useful to make small adjustments of body orientation during free-fall hunting. In all the videos studied here, it is possible to see that leopards make extremely fast tail movements during the fall. The role of the tail to change body orientation in mid-air was already determined in cats (Edwards, 1986; Fredrickson, 1989; Walker, Vierck and Ritz, 1998), primates (Dunbar, 1988), rodents (Bartholomew and Caswell, 1951) and lizards (Libby et al., 2012; Gillis, Kuo and Irschik, 2013). Moreover, wind tunnel tests illustrate that the fur of a felid's tail (*Acynonix jubatus*) exhibits significant aerodynamic drag, and numerical simulations revealed that the tail could impart significant angular impulse on the body by using these aerodynamic forces (Patel, 2015). The cheetah tail (and probably the leopard's tail too) could be employed effectively to stabilize rapid maneuvers even in mid-air (Libby et al., 2012 and references therein; Patel, 2015). Predatory vertebrates with arboreal adaptations, large tails, and some capability to generate significant aerodynamical forces are good candidates to present free-fall hunting behavior. Therefore, we can consider that free-fall hunting would be unlikely in extinct felids with short tails like those of the genera *Smilodon, Homotherium,* or *Megantereon* (Turner, 1997). Better candidates are felids and nimravids with a more arboreal design and long tails as *Pseudalurus*, *Proailurus*, and even *Hoplophoneus* (Turner, 1997). Moreover, from equations 2, 4, 6, and 7, it is possible to see that, if everything is equal, the probability of lethal blunt trauma increases with the prey's body mass. Therefore, for extinct predators that hunted prey larger than themselves, as it was suggested for *Smilodon* and several other sabretoothed felids (Turner, 1997), this behavior would be too dangerous.

Another very suggestive paleobiological implication is related to theropod dinosaurs and the origin of flight in birds. Our results imply that any adaptation enhancing the capability for righting and turning in mid-air during free-falling hunting would help avoid accidental collisions with a high probability of lethal blunt trauma. It was proposed that small theropods like *Velociraptor,* an agile, 20-kg, 1.5-m-tall biped with an active tail, might have been capable of aerial acrobatics beyond even those displayed by present-day arboreal lizards (Libby et al., 2012). The origin of avian flight required elongation of the theropods' forelimbs and the development of feathers from body integuments. Those features would be useful to generate aerodynamical forces with the forelimbs giving to some small theropods great control of body orientation and speed in mid-air (Dudley et al., 2007; Chaterjee and Templin, 2012). It was also suggested that among other biomechanical arguments, the climbing adaptations of maniraptorans such as *Sinornithosaurus* — including elongated forelimbs, swivel wrist joint, and recurved claws for grasping trunks, a caudally directed pubis, and a supporting stiffened tail end — give support to the arboreal hypothesis of the origin of flight (Chaterjee and Templin, 2012). It was suggested that maniraptorans like *Caudipteryx*, *Protarchaeopteryx*, and *Sinornithosaurus* might have had small proto-wings that most probably evolved as a safety device for arbore-

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al maneuvering to increase drag and reduce the impact of their fall (Chaterjee and Templin, 2012). All these features lead to the speculative scenario where some maniraptorans used free-fall hunting. Moreover, such behavior would be a candidate of selective pressure that in some stage improved the aerodynamical performance of wings and feathers, leading to the evolution of flying birds.

To assess the risk of predation in different situations as we did here could be useful to understand the predatory behavior of living animals. The methods presented here can also help assess the feasibility of paleobiological hunting scenarios proposed for extinct felids or other vertebrates.

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BIO-MECHANICS

Appendix 1. Data collected from videos

Video	Leopard — Cheetah Channel 2017	Kruger Sightings 2019	ACID 2018	Shock wave 2019	Shazal 2015
Time of the fall (s), measured from videos	0.7	0.5	0.8	0.7	1.0
Initial Height to the ground (m), measured from videos	3.51	2.84	3.88	3.39	4.15
Speed at the collision (m/s), estimated from traveled distance	7.2	6.2	7.7	7.0	8.0