Background to *Nature* manuscript 'Biomechanics of predator-prey arms race in lion, zebra, cheetah, and impala'

Some of the most athletic terrestrial animals are found in savannah habitats, where predators must chase down and catch prey. Since hunt outcome and success rate are critical for survival, both predator and prey should evolve to be faster and/or more manoeuvrable.

The purpose of the study was to determine how athletic animals need to be to survive – they must be athletic enough to be able to catch a meal or avoid being eaten, but not at the cost of other aspects of daily life, such as economical energy-efficient locomotion or the ability to defend themselves.

Wilson and his team developed specialised collars to track the animals and record every detail of their movement. The collars record the animal's location, speed, acceleration, deceleration and turning performance many times a second with pinpoint accuracy. Wilson then went to the savannah of northern Botswana and fitted collars to nine lions, five cheetah, seven zebra and seven impala. All animals in the study were wild and free-ranging. These four species were chosen because lions and cheetah often hunt prey in a one-on-one chase, and zebra and impala are the most common prey for each. A total of 5,562 high speed runs were analysed and the athletic capabilities of the predator-prey pairs, lion-zebra and cheetah-impala, were compared.

The team also took tiny muscle samples (biopsies) which were tested in their UK lab (RVC Structure and Motion Laboratory) to measure how powerful the animals' muscles were, since powerful muscles should result in better athletes (like a car having a more powerful engine).

They looked at five measures of performance:

1. maximum muscle power output and contraction speed (the engine).
2. how rapidly each species could accelerate and decelerate.
3. how rapidly each species could turn, which is based on grip and leg strength
4. how fast each species ran in hunts and the actual top speed recorded.
5. how frequently each species took a step, as each step is an opportunity to change direction or speed.

The team found that whilst cheetah and impala were much more athletic than lion and zebra, both predators were similarly more athletic than their prey. Their muscles were 20% more powerful, they were 38% faster, 37% better at accelerating and 72% better at decelerating. Predators and prey had similar turning performance.

In a hunt, the prey defines the speed and route while the predator attempts to pre-empt that strategy. It is in the predator's interest for the prey to run fast, since the predator is even faster. If the prey is running flat out (which one might expect to be a good means of escaping a predator) then its movement becomes predictable. It cannot speed up and can only make wide, gradual turns, which makes it easier for the predator to catch it.

If the prey runs more slowly, it has more options to twist and turn for avoidance of the predator and is hence less predictable. This is shown in the data where the prey are typically only running at about half of their maximum speed during hunts.

The predators are always running faster than the prey since they are catching it up; for them slowing to the speed of the prey so that they can follow the twists and turns is advantageous.

Whilst there were many hunts in the data, there were no instances of a collared predator hunting a collared prey, so we created a computer model to explore how conditions and tactics affect hunt outcome. A simulation was used to model the last two strides of a hunt after the predator has got close enough to capture the prey.

At the start of the simulation, the prey animal is a set distance, a few metres, ahead of the predator. With the first step forward, the prey has a certain area that it can reach. The area is limited by how rapidly each species can accelerate or turn (the animal's maximum acceleration) in each direction and a more athletic animal can reach a larger area.

Since the predator does not know what the prey is going to do, it is always one stride behind so it cannot respond to the prey animal's move until the second stride – by which point the prey has already taken another step in its chosen direction. Using the simulation, Wilson and his team were able to examine how hunt outcomes were affected by different prey speeds and different separations at the start of the hunt.

They also used the simulation to explore how athletic a predator and prey need to be. The more athletic the predator, the fewer hunts it needs to perform to be sure of catching the prey. If the prey is more athletic, it is more likely to escape. The results show that lions cannot sustainably hunt impala, which indeed they do not.

What the study found is that lower-speed hunts favour prey survival, as they give prey animals the opportunity to manoeuvre as much as possible. Predators must be more athletic than their prey to deal with the unpredictable trajectory of the prey and make a kill. The simulation shows that the best strategy for the prey is to turn at the last moment, making a movement the predator cannot follow. The faster the predator is going (because it is catching up quickly), the better for the prey.

Speed and hunting success are not the only factors in predator and prey survival; the predator must also be able to catch, hold and defend its prey. Both species must be energetically economical in how they move around their habitat, especially in a harsh environment such as the savannah.

The study was undertaken by Alan Wilson and colleagues in the Structure and Motion Lab at the Royal Veterinary College, University of London. The work was funded by ERC, EPSRC and BBSRC.

The group's work on cheetah locomotion is featured in the third episode of the BBC One Natural History Documentary "Big Cats" which is screened on Thursday 25th January, BBC One, 8pm.