of ocean tide, wet tropospheric delay, and wave height have large uncertainties relative to such measurements made in the open ocean. Furthermore, SSH or slope cannot be converted to gravity at a coastal point unless land gravity is also known. Efficient extraction of tectonic features from the increasing data volume of altimetry will require novel data processing strategies and gravity recovery methods (*9*, *10*).

In addition to geophysical studies, altimeter gravity is increasingly important for coastal terrain mapping on land and at sea with technologies such as GPS, LIDAR (light detection and ranging), and satellite imaging. These applications require a highly accurate model of Earth's level surface (geoid) from gravity measurements. A dedicated, small ship–based coastal gravity survey can deliver 1-mGal accuracy at 500-m spatial resolution (*11*), but the cost is high. If 1-mGal altimeter gravity accuracy can be achieved at this spatial resolution, coastal nations, especially at lower latitudes, will no longer need shipborne or airborne gravity measuring campaigns for purposes such as resource exploration and coastline topography determination.

Sandwell *et al.*'s results are a breakthrough in space-based marine gravity observation. The key factors driving this success are advances in altimeter technology (*10*, *12*), an improved processing technique (*3*, *7*), and a dedicated algorithm for deriving gravity and depth from altimetry (*1*, *8*). As CryoSat-2 continues to increase the coverage of satellite ground tracks to densify spatial coverage and several innovative altimeters are planned for launch (*10*), we will soon be able to detect even finer-scale gravity signatures that can benefit studies ranging from marine resource exploration to tectonic evolution. ■

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The hunt is on. Cheetahs reach famously high speeds during hunting, but Scantlebury *et al*. show that it is the search for prey rather than the chase itself that is energetically more costly.

ECOLOGY

How large predators manage the cost of hunting

For pumas and cheetahs, seeking prey is more energetically costly than the subsequent chase

By **John W. Laundré**

Being a large carnivore is not easy. First, there is the food, the energy they need to survive, which by definition consists mainly of other animals. This means that meeting daily energetic needs is not as easy as just going out and gathering plants that are waiting around to be found and eaten. Large carnivores often prey on animals that are bigger than themselves and that try to avoid being killed. Foraging by carnivores becomes a two-player game of stealth and fear (*1*), making it more difficult and thus energetically costly for carnivores to catch enough to stay alive. Large carnivores must balance the energy spent seeking and subduing prey with the energy they get back when they catch something—which does not happen as often as one might think (*2*–*4*). Two reports in this issue, by Scantlebury *et al.* (*5*) on page 79 and by Williams *et al.* (*6*) on page 81, look at how two carnivores, cheetahs (*Acinonyx jubatus*; see the first photo) and pumas (*Puma concolor*; see the second photo), tread the fine line of energy losses and gains in order to survive.

The carnivores investigated in the two studies seek prey in very different ways. Pumas are sit-and-wait hunters, whereas cheetahs typically chase their prey at high speeds. The results of the studies should thus help to elucidate the effect of energetic demand on hunting style.

There have been ample studies of the energetics of carnivores. However, most attempts to calculate the energetics of large carnivores have not explicitly determined the specific energy necessary for seeking and subduing prey. Most have relied on estimates of metabolic rates under laboratory conditions (*7*, *8*) or velocities and distances traveled over 24 hours based on telemetry or Global Positioning System data gathered from wild animals

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with collars (*9*, *10*). Williams *et al.* and Scantlebury *et al.* instead used more specialized techniques to measure specifically the energy that a carnivore expends during the critical phases of searching for and subduing prey. The most ingenious was the use by Williams *et al.* of a new SMART (species movement, acceleration, and radio tracking) collar that differentiated among various activities such as resting, eating, and running. The results help to understand how the two species have evolved to compensate for these high-energy-demand activities and have consequences for the conservation of these species.

Both studies concur that seeking prey is much more energetically costly than subduing the prey. Intuitively, one would think that the extreme physical exertion of chasing and pouncing on prey would far outweigh the searching process. As both studies point out, however, although subduing prey is energy-intensive, the time spent doing this is short. Carnivores either quickly capture their prey or give up. Furthermore, Williams *et al.* found that pumas adjust their energy investment based on prey size, not overexerting themselves on smaller prey. Of interest, but not addressed in these articles, is whether carnivores take into consideration the amount of energy they are willing to expend for a capture before giving up on the chase. If they do, could their current energetic state, that is, the time since they last ate, have an effect on their behavior? Will they end a chase sooner or be less willing to attempt subduing more energy-intensive prey depending on how long ago they have last eaten? Such data would increase our knowledge of whether carnivores are regulating their energy expenditures even more than these articles suggest.

"Pumas are sit-and-wait hunters, whereas cheetahs typically chase their prey at high speeds. The results of the studies should thus help to elucidate the effect of energetic demand on hunting style."

Because seeking prey is the more energy-intensive activity, both studies propose that these species have evolved ways of reducing this demand. Pumas can substantially reduce the energy demand of seeking prey with their sit-and-wait approach, as do most felids—except cheetahs. Cheetahs, and probably other carnivores that chase their prey, opt for minimizing the time they are mobile and seeking prey. Scantlebury *et al.* point out that kleptoparasitism—the theft of prey by other animals, in this case by lions and hyenas—increases how often or how long carnivores such as cheetahs have to seek animals. However, they note that if prey abundance is high, cheetahs can quickly find additional animals to pursue, reducing the impact of kleptoparasitism to an acceptable level.

The overall conclusion of the two studies is that evolution has honed the behavior of these two carnivores to maintain the balance of energy needed in finding and subduing a reluctant food source. Both authors caution, however, that human activity can disrupt this balance. Any human-caused loss of vegetative cover may make it harder for a sit-and-wait predator to sneak up on its prey. Human-reduced prey abundance would require predators to expend more energy in the costly search for prey to hunt. In either case, these changes can increase the energy that predators expend in both seeking and subduing prey, and thus threaten their survival. In this case, conservation of adequate habitat and prey abundance become paramount in efforts to conserve large carnivores.

The two studies greatly increase our understanding of the energetic demands of large carnivores, but there is still more to do. The ecological concept of the landscape of fear, where prey alter their habitat use based on predator lethality, has a flipside for the predator, the landscape of opportunity (*11*). In this model, in some habitats, predators have an easier time capturing prey (*12*), thus requiring less energy expenditure. Incorporating how carnivores use their landscape of opportunity to minimize energy expenditures for seeking and subduing their prey will go even further to help us understand how large carnivores manage and manipulate their role in the cat-and-mouse game of life. ■

Stealthy hunter. Pumas hunt by stalking and ambushing their prey. Williams et al. show that—as in the case of the cheetah—seeking prey is more energetically costly than subduing the prey.

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