Quick guides

# Lions

**Craig Packer**

***What are lions?*** The largest cats in Africa, lions are about the same size as tigers. Modern lions descend from the extinct cave lion (*Panthera atrox*), which once ranged more widely than any mammalian species. Modern lions dispersed from Africa to Asia about 100,000 years ago, but Asiatic lions are now restricted to a small part of Gujarat in western India. African lions once ranged from the Atlas Mountains to the Cape of Good Hope, but both the Atlas lion and the Cape lion no longer exist in the wild. Although there are slight genetic differences between lions in eastern, western and southern Africa, all African lions are considered to belong to the same subspecies.

Lions prefer prey that range in size from goat-sized gazelle to Cape buffalo. Litter size is typically two or three cubs; offspring are weaned by 6–8 months but remain dependent on their mothers for about two years. Females first give birth at the age of 3–4 years and show marked reproductive decline by the age of 14 years. Males typically start breeding by 4–5 years. In the wild, maximum lifespan is 19 years for females and 15 years for males.

Uniquely among felids, female lions form stable social groupings ('prides') of up to 22 females. Male lions form coalitions of up to 10 males that may control several prides, either simultaneously or sequentially. Male lions are also unique among felids for growing conspicuous manes.

Lions are the best-studied big cat species, being the focus of long-term research in Tanzania, Kenya, Botswana, Namibia, South Africa and Zimbabwe, with additional studies in Benin, Cameroon, Ghana, Mozambique and Zambia.

***Why do lions live in groups?*** The traditional explanation for lion sociality has been cooperative hunting, but lions do not hunt as cooperatively as believed. Consequently, individual lions do not always feed better in larger groups, because a single group member often does most of the hunting while the rest just watch. Communal cub rearing confers substantial benefits: groups of mothers can successfully defend their cubs against an infanticidal male, whereas a lone female has no chance one-on-one. But most other felids — for example, leopards, cougars, tigers, bobcats and lynx — are also infanticidal, yet they are all solitary.

The true hallmark of lion sociality is their joint defense of a territory (Figure 1). Karen McComb measured the responses of females to recorded roars of unfamiliar females. A roar is a territorial display, and the females responded according to the odds: if a lone female heard the roar of a single female, she recruited distant pridemates, but a group of three females immediately approached the loudspeaker. When exposed to a roaring trio, real trios again recruited help, while quintets quickly approached. The real females moved to oust the invaders as long as they outnumbered the strangers by at least two individuals. Jon Grinnell found a similar sense of 'numeracy' in males, but they sometimes approached even when outnumbered three to one — probably because males have such a brief opportunity to father offspring and must protect their pride at all costs.

Possessing a high quality territory is essential for successful reproduction, and as a pride grows it is able to annex particularly valuable landscape. Anna Mosser developed a map of lion 'real estate', based on localized reproductive rates and found that river confluences were the most important landscape features. Migratory herbivores are reluctant to cross tributaries because of the risk of ambush and are often funneled into the confluences, where lions make most of their kills. Water flow also scours riverbeds most deeply at confluences, leaving the most persistent waterholes and promoting the densest vegetative growth. Consequently, prides that control the most confluences leave the greatest number of descendants, and larger prides maintain control of the best habitat.

The savannas are the most heterogeneous of felid habitats; lions live at higher densities than other species of big cat and thereby face the most intense competition for good habitat. Thus, only lions can benefit from banding together and defending highly valuable landscape features.

***Why do male lions have manes?*** The mane may either serve to shield a male's neck during fights with other males or to indicate the male's 'quality'. The mane is unlikely to be a shield, as neck wounds are no more common than on other parts

Figure 1. A gang attack during an intergroup encounter in Serengeti lions.

Lions are at their most cooperative when fighting against outsiders. Females form prides to defend joint territories; males form coalitions to gain exclusive access to female prides. (Photo: Ingela Jansson.)

of the body nor are neck wounds more likely to be fatal — even in females and maneless sub-adult males. Instead, the mane appears to indicate 'quality': males may lose their manes after being seriously injured, and dark-maned males have higher testosterone levels, are more likely to recover from physical injury and their offspring have better survival. Thus, mane length indicates recent fighting success, and mane color conveys information about male aggressiveness and potential reproductive success. Peyton West set out pairs of life-sized toy lions that differed in either mane length or mane color. Males approached the 'weaker' member of the pair as indicated by a shorter or lighter mane. In contrast, females were indifferent to mane length, but were much more attracted to dark manes than to blonds.

Variation in a sexually selected trait generally results from the inherent costs of expressing such elaborate physical characteristics so that only the highest-quality males can carry the most exaggerated traits. Infrared thermography revealed that maned male lions suffer greater heat stress than females, and males with darker manes are hotter than males with blond manes. Consistent with these findings, males with darker manes have higher proportions of defective sperm, and eat relatively small meals in hotter weather. These costs are burdens that only superior males can bear; for inferior males, a dark mane would inflict physiological costs that outweighed the reproductive benefits.

### *What is the future of the lion?*

Habitat loss has restricted lions to 10% of their former range, and many of the surviving populations face intense conflicts with rural villagers. Substantial numbers of lions are killed each year in retaliation for livestock depredation and man-eating. Lions are an important trophy species for the sport-hunting industry but have been seriously over-harvested in most countries. There is considerable demand for lion parts in Nigeria and growing concern that lion bones may replace tiger bones in traditional Chinese medicine.

Conservation efforts are dwarfed by the lions' enormous range requirements (individuals can disperse >400 km), and the large size of key reserves (for example, Tanzania's Selous Game Reserve is ~55,000 km$^2$). Lions are well managed in South Africa where the parks and reserves are all fenced, but fencing the national parks in the rest of sub-Saharan Africa seems infeasible. Lions along Namibia's Skeleton Coast and in Zimbabwe's Save Valley Conservancy were rescued from near elimination by intensive conservation efforts, but recovery in Namibia led to renewed conflicts with local people. Intensive efforts to engage pastoralists in lion conservation in Kenya are so far successful, but only protect a few dozen lions; to remain genetically viable, a population should number at least a thousand.

Faced with these trends, the long-term future of the lion is bleak. African countries are reluctant to place restrictions on trophy hunting, human populations continue to grow, wildlife habitat continues to shrink, Chinese influence in Africa is expanding, funding for national parks is shrinking, and the costs of conserving even a single lion are growing. In the long-term, the lion seems doomed to the same fate as the tiger or the panda, except for a few well-protected areas like the Serengeti or Kruger.

### *Where can I find out more?*

Antunes, A., Troyer, J.L., Roelke, M.E., Pecon-Slattery, J., Packer, C., Winterbach, C., Winterbach, H., Hemson, G., Frank, L., Stander, P, *et al.* (2008).The evolutionary history of lion: Integrating host/pathogen molecular genetics. PLoS Genet *4*, e1000251. doi:10.1371/journal.pgen.1000251.

Grinnell, J., Packer, C., and Pusey, A.E. (1995). Cooperation in male lions: kinship, reciprocity or mutualism? Anim. Behav. *49*, 95–105.

IUCN. (2006). Conservation Strategy for the lion (Panthera leo) in Eastern and Southern Africa, http://www.felidae.org/JOBURG/Lion_E_Sweb1.pdf.

McComb, K.E., Packer, C., and Pusey, A.E. (1994). Roaring and numerical assessment in contests between groups of female lions *Panthera leo*. Anim. Behav. *47*, 379–387.

Mosser, A., and Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, Panthera leo. Anim. Behav. *78*, 359–370.

Packer, C. (2009). Rational fear. Nat. Hist. *119*, 43–47.

Packer, C., Scheel, D., and Pusey, A.E. (1990). Why lions form groups: food is not enough. Am. Nat. *136*, 1–19.

Packer, C., Kosmala, M., Cooley, H.S., Brink, H., Pintea, L., Garshelis, D., Purchase, G., Strauss, M., Swanson, A., Balme, G., *et al.* (2009). Sport hunting, predator control and conservation of large carnivores. PLoS ONE *4*, e5941. doi:10.1371/journal.pone.0005941.

West, P.M. and Packer, C. (2002). Sexual selection, temperature and the lion's mane. Science *297*, 1339–1343.

Department of Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Circle, St. Paul, MN 55108, USA.
E-mail: packer@umn.edu

# Pycnogonids

**Matthew Cobb**

***What are pycnogonids?*** Also known as 'sea spiders', they are bizarre-looking marine arthropods whose name means 'dense-knees'. Most species have very long, thin legs and extremely slender bodies — essentially a combination of slightly distended leg-bearing segments (Figure 1). Many species look as though they are just a tangle of cream or yellowish-brown appendages, hence their old name — 'nobody crabs'. They are, however, neither crabs nor spiders.

***What do they look like?*** They have a head region, the cephalosoma, which always carries a proboscis, and usually has four eyes and four pairs of appendages: chelifores, palps, the first pair of legs, and structures called ovigers, used in reproduction. Some species lack eyes and the number of appendages varies. Although most species have four pairs of legs, some have duplicated segments, and have five or six pairs. The slender body means that organ systems, including the gonads, have been displaced into the legs. They have an extremely large surface area for their size, and are able to directly absorb oxygen from the water without any specialised respiratory system.

***Why are they interesting?*** They look weird, and we know little about their biology. For over 130 years, there has been a long-running argument about their position on the tree of life. This dispute raises fundamental questions about the evolution of animals, going back to the earliest arthropods and the Cambrian Explosion, over 500 million years ago. T.H. Morgan, the founder of *Drosophila* genetics, studied sea spider ontogeny and phylogeny for his PhD in the late 1880s. At the time, pycnogonids represented a challenge because their relation to other arthropods was unclear. Morgan was uncertain whether they represented an ancient arthropod form, or whether they were more closely related to the chelicerates. That debate is still very much alive.

***What are the arguments?*** There are over 1,300 species of pycnogonid and, on the basis of morphology,