obese. Applying an understanding of nutritional and evolutionary theory to the modern human nutritional dilemma has turned out to be very enlightening indeed.

Who have been your most important mentors? Two people have had the greatest impact on my career. The first was the late Reg Chapman as my PhD supervisor. Reg and his wife Liz Bernays were inspiring, selfless and incredibly tolerant. I couldn't have asked for a better supervisory team. The second was the late Sir Richard (Dick) Southwood, a distinguished ecologist and my Head of Department at Oxford for many years. Dick was an extraordinarily effective academic leader. Both Reg and Dick nurtured and brought out the best in their people and encouraged intellectual bravery. They both sent presents when our children were born. I have tried to emulate them, but cannot hope to have Dick's facility for remembering the names and personal details of every member of academic and general staff, graduate and undergraduate student who was ever in his charge.

What was the most laborious experiment you have ever done? There have been many, but the first experiment I did as a PhD student must be close to the top. I sat in a heated room and watched 10 locusts feed for six days and six nights (under red light), recording the timing and size of every meal eaten and every defaecation. My supervisors lived nearby in Kensington. Reg took over for a few hours each morning while Liz would cook me breakfast and I'd grab an hour's rest. For entertainment I had a small tape recorder, one ear plug and a single Talking Heads tape, which I listened to continuously. I ended up with a dataset that I mined for years, a deep understanding of locust behaviour, a toe-hold on the cliff face of nutritional biology, a sore ear, and, despite it all, a love of Talking Heads.

Is field work fun or hard work? Both, but it is essential if you are to have a complete understanding of biology. Sometimes things work spectacularly well but more often they don't. My favourite example was a trip to Utah with Greg Sword, Pat Lorch and Iain Couzin to study why large flightless Mormon crickets form massive migrating bands extending kilometres. In a week we managed to conduct a series of experiments proving that the crickets are on a forced march to find limiting protein and salt. The reason they keep moving is because of the threat of cannibalism: the most abundant sources of protein and salt in the habitat are other crickets and if you don't keep moving you get eaten. (A colleague later mentioned that this was a metaphor for academic life.)

The discovery that cannibalistic encounters drive mass movement provided a new mechanism for collective movement, which we now know applies also to locusts. Greg and Pat had had a previous trip where a PhD student-to-be of mine, Gabe Miller, had joined the team as a field assistant before starting his research project with me in Oxford. Gabe had secreted a gorilla suit in his field gear. Pat lured Greg to a patch of sage brush under the pretext that a radio-collared cricket was there. Greg, wearing head phones and waving the radio antenna, homed in on the transmitter, whereupon Gabe leapt out beating his chest and screaming. Greg ran away very fast indeed. Wish I'd been there.

What do you do to relax? I conduct practical experiments in freshwater and marine nutritional ecology. Some of my closest scientific colleagues are also keen anglers. To give an indication of our dedication, one mayfly hatch I was walking with Dave Raubenheimer through the Wychwood forest in Oxfordshire on the way to fish for trout from a skiff. Dave had recently come out of plaster for a snapped Achilles tendon (an injury gained while playing badminton in the back garden with his children — a dangerous pursuit). As we walked, Dave tripped on a rock and we both heard the tendon snap again. It was the trauma ward for Dave, either now or after the day's fishing. Dave hopped on to the boat and we had an extraordinary day's fishing.

School of Biological Sciences,
Heydon-Laurence Building, A08,
University of Sydney, Sydney,
New South Wales 2006, Australia.
E-mail: stephen.simpson@bio.usyd.edu.au

Quick guide

Fission–fusion populations

Iain D. Couzin and Mark E. Laidre

What is fission–fusion and why is it important? Grouping among animals is ubiquitous, from swarms of insects, schools of fish and flocks of birds to herds of ungulates, troops of primates, and vast interconnected human urban settlements. In many grouping species, across genera and scales of organization, group formation is a highly dynamic process: group size and composition change frequently within the lifetime of members as groups split (fission) or merge (fusion) (Figure 1). The timescale over which such fission–fusion dynamics occur, the degree to which individual group-members control the process, and the influence of environmental factors differ among species, and often within species as environmental conditions or individual requirements change.

The spatial and temporal aspects of how animals move and interact is of fundamental importance to some of the most pressing questions in biology: tracking disease transmission, determining how genetic and cultural information spread within and among inter-connected populations, predicting the invasion dynamics of introduced species, and understanding the evolution of animal sociality, including that of our own species.

How do the rates of fission and fusion affect grouping? The competing processes of group coalescence and breakup means that when the rate of fusion is low relative to that of fission, groups tend to be unstable, there are many isolated individuals within populations, and the probability of finding larger groups tends to decrease exponentially with group size. When the rate of fusion is high relative to that of fission, however, the group-size distribution often exhibits a relatively long tail (power law-like) and there is no characteristic group size in the population (as, for example, in marine pelagic fish and some large herding

Figure 1. Fission–fusion dynamics in Merinos d'Arles sheep, *Ovis aries*. (Photo: Simon Garnier.)

vertebrates like buffalo). Regardless of its exact form, for many species that exhibit fission and fusion, including social spiders, seals and herding ungulates, the distribution of group sizes is strongly skewed.

Are there parallels between fission–fusion processes in biology and physics? Yes. Populations of organisms, like schooling fish or herding ungulates, consist of a very large number of interacting entities that bear important similarities to some physical processes, such as the spontaneous formation and dissolution of charged particle aggregates. Modifications of such physical models to simulate social interaction 'forces' have suggested, remarkably, that only relatively few biological and physical details may determine the distribution of group sizes produced by fission–fusion dynamics. Similar simple models have revealed how differences among individuals within populations (in activity patterns, motion characteristics or social interactions), result in a spontaneous 'self-sorting' whereby individuals tend to form disproportionately close associations (and thus groups) with others that are similar to themselves. This could allow individuals to spontaneously group with others that have similar physiological or behavioral needs, and may also play a role in the evolution of cooperative behaviors among organisms that lack the cognitive abilities required for active assortment within populations.

If there is no well defined group size, where does that leave optimal group-size theory? It has long been known that there are costs and benefits of group membership. Individuals in large groups may benefit from enhanced protection from predators, but also suffer increased competition for food. It has been argued, therefore, that there should be a relatively well-defined 'optimal' group size for any prevailing ecological condition. The dynamic and probabilistic nature of grouping in many fission–fusion populations suggests that conditions, including internal state, social interactions, and the environment, may all play a role in generating a much more complex, and frequency-dependent, optimization problem for individuals.

What role does the environment play? Fissioning is often a response to resource limitation permitting decreased competition for unpredictable and patchy food resources. Aggregation, on the other hand, can confer increased protection from predators. Patterns of association can change over multiple timescales, from slow seasonal adjustments as in many grouping animals to daily patterns of diurnal fission for feeding and nocturnal fusion for protection.

Are fission–fusion societies common in mammals? The term 'fission–fusion society' was coined by the biologist Hans Kummer while he was unraveling one of the most complex mammalian social organizations: the multi-level societies of hamadryas baboons. In such societies, there typically exist highly structured social relationships with fission–fusion events occurring upon predefined societal 'seams', such as those between different harem, or family, groups. Kummer discovered that, within huge troops of up to 750 individuals, there existed several types of sub-groups that split and fuse over the course of a single day. The lowest level, the 'one-male unit', is composed of a mature male and a permanent harem of females. Several one-male units combine to form a 'clan' in which the males sometimes engage in cooperative defense against predators and intruding bachelor males. A collection of clans together forms a 'band', which stays together for part of the daily foraging expedition. And ultimately a 'troop' is formed by a number of clans that unite at the sparsely distributed water sites and overnight together at a sleeping cliff.

The fission–fusion social structure of hamadryas baboons is not, however, unique among mammals: species of cetaceans and ungulates, as well as hyenas and bats, also have such societies. African elephants, for instance, form sophisticated, multi-scale groupings with highly cohesive low-level units (between mother and calf) and increasingly ephemeral aggregations at higher levels. Recently, several researchers have even suggested that all mammals exhibit some degree of fission–fusion dynamics. If true, then the term fission–fusion might best be used to characterize a continuum rather than a single modal social organization.

Do insects exhibit fission–fusion? Many group-living insects, including cockroaches, locusts, social spiders, and social caterpillars live in fission–fusion populations. Eusocial ants, which were once thought to live exclusively in stable, long-lived colonies, also exhibit pronounced fission–fusion behavior, with nests splitting and merging according to ecological contingencies. Some species exhibit substantial worker exchange among nests, like the invasive Argentine ant (*Linepithema humile*). This species, in particular, forms 'supercolonies' in their introduced range, with individuals freely mixing among a vast network of nests that extends over hundreds of square kilometers.

What about humans and our closest evolutionary relatives? The most fluid societies of any nonhuman primate are found among chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), humanity's nearest living relatives. Chimpanzee communities, for instance, are rarely seen together as a whole. Instead, subgroups of various sizes constantly coalesce and split based on moment-to-moment foraging and socializing needs. Subgroups of adult male chimpanzees separate from the group to cooperatively hunt mammalian prey or to patrol their border, and male-female dyads split off from the group to engage in sexual consortships with minimal mating competition. As a consequence of such fission–fusion processes, the composition of traveling chimpanzee parties is highly variable, often changing by the hour.

When it comes to our own species, there is no doubt that, by nature, we form fission–fusion societies. And nor is this merely a reflection of our current, highly mobile lifestyle within industrialized settings. More than 99% of human history was spent in a hunter-gatherer existence, characterized by dynamically shifting social groupings at multiple levels. At the highest tier in hunter-gatherer societies is the ethno-linguistic group or 'tribe', formed by several local 'bands' that fuse together when resources like water are clustered during dry seasons. Bands themselves, which are made up of around 30 individuals, break up into smaller foraging parties during daily forays out from a base camp. While some individuals remain at the camp to watch over youngsters and tend the old or injured, the foraging parties gather edible plant material and hunt animals, afterward bringing the bounty back to a central place for sharing and redistribution.

Hunter-gatherer societies exhibit division of labor, though mostly between the sexes and not to the extent of the highly specialized castes of social insects. Hunting, for instance, is typically — but not universally — done by men, while gathering is done by women and in part by men too. Pair bonds, non-existent in the promiscuous chimpanzees and bonobos, enable men and women to assume distinct but complementary ecological roles, splitting apart during the day and then pooling their assorted resources when they convene at night. Aside from such ecological reasons for fission–fusion among hunter-gathers, social reasons also abound. One of the most common is verbal disputes and fighting, which can result in individuals switching camps. The Hadza of Tanzania insist that fissioning into smaller camps is a surefire route to 'less bickering'.

What does gossip have to do with fission–fusion? Gossip, in the strict sense of talking about third parties who are elsewhere at the time of the dialogue, appears to be uniquely human. Of even greater interest, most of our species' conversations — over two-thirds by some study estimates — focus on gossip. But why is gossip necessary? Far from being mere small talk, gossip serves myriad vital functions within our fission–fusion societies, both at the individual level and at the group level. Gossip can facilitate social cohesion in the face of repeated separations, reminding individuals of the bonds they have with distant others. And it can also allow information to percolate through the group about the trustworthiness of each member, enabling listeners to keep track of others despite limited first-hand observation. Gossip, therefore, and maybe even language more generally, may have evolved specifically as an adaptation to the highly fission–fusion-oriented societies of our hunter-gatherer ancestors.

Where can I find out more?

Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., Connor, R., DiFiore, A., Dunbar, R.I.M., Henzi, S.P., *et al*. (2008). Fission-fusion dynamics: new research frameworks. Curr. Anthropol. *49*, 627–654.
Gueron, S. and Levin, S.A. (1995). The dynamics of group formation. Math. Biosci. *128*, 243–264.
Hölldobler, B. and Wilson, E.O. (2008). The Superorganism: The Beauty, Elegance, and Strangeness of Insect Societies (New York: W.W. Norton).
Kummer, H. (1995). In Quest of the Sacred Baboon: A Scientist's Journey (Princeton, NJ: Princeton University Press).
Marlowe, F.W. (2005). Hunter-gatherers and human evolution. Evol. Anthropol. *14*, 54–67.
Niwa, H.-S. (2004). Space-irrelevant scaling law for fish school sizes. J. Theor. Biol. *223*, 347–357.

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA.
E-mail: icouzin@princeton.edu, mlaidre@princeton.edu

Primer

Evolution of sound localisation in land vertebrates

Christine Köppl

Pinpointing where a sound comes from may appear trivial to you. After all, we do it constantly without even thinking about it. Yet, by the time you become aware of that bird call from the tree outside the window or the footsteps of your child running down the stairs, your brain has been hard at work deducing the directions these sounds came from by using a number of different cues. Unlike vision, the sense of hearing cannot rely on a spatial image of the external world being projected onto the primary receptor surface and relayed to the brain. The inner ear works much like a spectrum analyser, with individual receptors being exquisitely sensitive to a narrow part of the audible frequency range, but conveying no information about the spatial origin of that sound. Thus, the onus is on the brain: it needs to determine where sound came from using indirect cues. How do humans and other animals do that? Until recently, it was thought that we understood at least one particular aspect of sound localisation — the neural processing of interaural (between the ears) time differences — fairly well. But conflicting results from work on birds and mammals has sparked a lively debate about whether there is only one or perhaps two fundamentally different mechanisms. I will use this specific example to illustrate how a broader look at the evolution of sound localisation and hearing in general can be instructive in identifying the constraints on specialised neural circuits and in deducing their evolutionary histories.

Let's get physical: the basics of sound localisation cues

Sound localisation has a lot to do with the relative dimensions of the listener and the sound waves to be localised, so some basic facts about the physics of sound propagation and diffraction need to be appreciated. The physical cues that are widely known to be