easily fill an article or, indeed, a monograph. This systematic screen for developmental mutations has revolutionized developmental genetics, and it provides a veritable Who's Who of developmental regulatory genes, each of which has given rise to an entire cottage industry of research. Of course the two papers also led directly to a Nobel Prize, which just means that they have good taste in Stockholm.

I also have a favorite lecture. The clear choice is Francis Crick in 1962, presenting genetic studies on the triplet nature of the genetic code in a blackboard lecture without slides. The clarity, elegance and excitement of this talk that guided the audience through the logic of the experiments has remained vivid in my memory ever since.

Can you see any major problems in the biological research enterprise? There are many, of course. I want to mention one that, at least at some level, can be influenced by the research community itself, rather than depending on society as a whole. It is the imbalance, as it appears to me, between jobs available at different stages of a scientist's career. Most universities, I am told, are looking for graduate students. Most labs, I know, are looking for postdocs. Yet after completing postdoctoral training, many biologists find that a suitable job for the next stage of their career is beyond reach. The most accomplished are still in wide demand, but many competent young scientists find themselves in precarious circumstances. It seems clear to me that 'the system' has arranged it in such a way that there are too many openings for postdocs and too few for subsequent long-term employment. I have no easy solution — or even a difficult one — but I believe that as a community we need to face this problem if we want to see a healthy scientific enterprise in the long run.

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Quick guide

Hummingbirds

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What is a hummingbird?
Hummingbirds (Family Trochilidae) are some of the most spectacular New World birds and are often referred to as jewels because of their bright, iridescent colouration and their small size. The Indians of Central and South America called them ourissa (rays of the sun) and their scientific names often reflect thoughts of the sun, stars and precious stones. Most of the more than 330 species are small, typically weighing just a few grams. The smallest is the Bee Hummingbird, *Calypte helenae*, from Cuba which, at just two grams, is the smallest bird of all; of its nine centimetres from tip to tail, its bill accounts for over a centimetre and its tail more than six centimetres. Hummingbirds can come in larger sizes though: the giant of all hummingbirds is *Patagona gigas*, from Chile, which at 21–22 centimetres in length is the size of a starling.

The name hummingbird comes from the 35–100 Hz sound made by the rapid beating of their wings as they fly; a three gram hummingbird beats its wings an astonishing 50–70 times per second. Males are polygynous and sometimes promiscuous, and during their courtship displays an additional 3–10 kHz sound can be produced by air moving over the tips of modified feathers at the end of their wings.

Where would I find one?
Hummingbirds originated in the Andes and have since spread throughout the Americas. Their fossil record is poor, with only a few bones from the Quaternary of Central America, although a recent finding in clay pits in Germany would suggest that hummingbird-like animals existed in the Old World 30–34 million years ago. Whereas most of the North American species overwinter in the southern United States or points further south, making short migrations to breed, several species migrate over two thousand miles to the north to breed. The rufous hummingbird wins the long distance record, making an annual journey from northern Mexico as far as Alaska, following the chain of mountains north, just as the snow melts.

Although one usually associates these small birds with warm places, they are better able to deal with variation in temperatures than many other small animals. In the middle of May, for example, when the rufous hummingbird arrives at its breeding grounds in the Canadian Rocky Mountains, the temperatures are still often in single figures (°C) and the ground sometimes covered in snow. Even a few weeks later, when temperatures have warmed up, females often have to contend with snowfall in the middle of incubation. Even in these conditions, the two pea-sized eggs are kept at least 25°C warmer than ambient temperature, thanks to the female's body heat, around 39°C, and the effective nest insulation. Yet by July, when the adult males leave the breeding grounds on their journey to Mexico, the midday temperatures are often above 30°C. They are able to deal with cold temperatures because their feathers provide some of the best avian insulation, with more feathers per inch of surface than other small- to medium-sized birds. Furthermore, they can go into torpor to lower their metabolic rate, maintaining body temperature at about 12°C when he ambient temperatures drop below 10°C.

The long distance migratory hummingbirds also require rapid fat acquisition prior to departure and during the stopovers during the journey. These birds can gain as much as 72% of their body weight in fat before migrating (fat is used in preference to carbohydrate because it provides twice the efficiency per gram of weight lifted). They have the most metabolically active liver known, with the highest levels of enzymes

Figure 1. Two views of a hovering female rufous hummingbird.

for lipid synthesis along with extremely high rates of intestinal glucose transport, which results in very dilute excreta, invaluable for a nectarivorous animal ingesting large quantities of water in its food. Quite how they are able to produce highly dilute urine is still not known, but it appears that their renal morphology and physiology is more like that of nectarivorous bats and freshwater amphibia than that of non-nectarivorous birds.

What are they known for? The first thing one notices about a hummingbird is its diminutive size and all-over iridescent plumage, often coupled with especially striking throat (gorget) feathers, which males use to signal to conspecifics. The next obvious feature is their ability both to hover — for feeding at flowers and in insect swarms — and to manoeuvre at speed, including upside down and backwards.

They achieve their remarkable agility in flight by having a wing structure unlike that of any other birds, which articulate their wings from shoulder, elbow and wrist: hummingbirds' wings articulate only from the shoulder. The rigidity of the wing is not dissimilar to that of an insect and enables similar flight characteristics. Their flight muscles comprise 25–30% of their total body weight, a higher proportion than for any other bird, and one has to look to the Diptera for a higher density of mitochondria in flight muscles (over 30% in hummingbirds, 40% in flies). While hovering, the small hummingbirds have the highest known mass-specific metabolism for a vertebrate of around 40 ml oxygen per gram per hour (falling at rest to approximately 3 ml oxygen per gram per hour).

Adult hummingbirds rarely figure in the diet of other animals, although on occasion they may become tangled in spiders' webs or get taken by frogs, fish, raptors and other birds, or, perhaps most surprisingly, praying mantids.

What about their role as pollinators? All hummingbird species are primarily nectar feeders, although they will also catch insects or lick sap. Consequently, like nectar-feeding insects, they are pollinators, and it is suggested that they engage in similarly specialised 'lock-and-key' relationships with the plants on which they feed. For example, the preponderance of red flowers in California may be a result of hummingbird pollination, as moth-pollinated flowers are often white.

At least some hummingbird-pollinated flowers have evolved from species pollinated by Hymenoptera, such as bees. Typically, these flowers offer relatively large quantities of dilute nectar, tend to be scentless, and have a corolla that allows easier access to hummingbirds than to other possible pollinators. The way pollen is delivered also seems to vary with pollinator: hummingbirds are more efficient at pollen transfer as they preen less than do bees, so the flowers they feed from may deliver pollen simultaneously with nectar, whereas bee-pollinated flowers tend to deliver pollen more gradually. Some species of plants produce flowers that exploit the relationship between hummingbirds and the flowers they pollinate: *Lobela cardinalis*, for example, has flowers that mimic the morphological characteristics of hummingbird flowers but that offer no nectar.

What can a hummingbird do with a very small brain? Although the rufous hummingbird has a brain approximately the size of a grain of rice, it puts it to rather good use. Firstly, it appears that migrant hummingbirds are highly philopatric — that is, they return from the south each year to the same or neighbouring breeding territories in north-western or north-eastern North America. They also appear to remember where they have visited hummingbird feeders along the way: the reminder for garden owners to put the feeder containing sucrose solution out is often a bird hovering around the place the feeder was hung the previous year. Secondly, they have been shown to remember information on a more local scale, avoiding flowers they have recently emptied and returning to flowers they have left still containing food.

Where can I find out more?

Birds of North America Online, http://bna.birds.cornell.edu/BNA/

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