extraordinary financial pressures that the NIH currently experience threatens the US science enterprise. This not only puts extreme pressure on established scientists but makes it very difficult for young people to develop their research programs. The NIH have put in place mechanisms to make it easier for young people to obtain their first grant, but all this does is get new researchers through the first four years of their careers. Renewing this first grant is extremely difficult. Young scientists must compete with the entire scientific community for an extremely limited amount of resources.

Unfortunately, there are only two solutions to this problem: putting more money into research or shrinking the research enterprise. At the moment the US government is pursuing the latter. The result is trivial to forecast. The US science enterprise will shrink dramatically, while at the same time countries like India and China who heavily invest in research will become the world's science and technology leaders. It seems to me that every American, Democrat or Republican, should be concerned about this and make it their highest priority and that of their elected officials to maintain the US's leadership position in science and technology development. Saving a buck or two by cutting the budgets of funding agencies such as the NIH or NSF (the NIH's and NSF's research budgets are small change compared to other budget items; e.g. defense) is really short sighted and, importantly, the impact is long term. Firstly, people with career aspirations in science are going to be pruned. The days of pruning come when study sections meet — either for the first grant or the first renewal — and then when university promotion committees meet, by which time the aspiring scientist is 35+ and in need of a new career. Secondly, seeing established and starting scientists alike struggle so much to secure funding and make a living as scientists will turn off the coming generations from research.

What kind of research should we be funding? I firmly believe that real medical breakthroughs come out of basic research. This is why we must make funding basic research a priority. As we mostly rely on tax dollars to conduct this research it is our responsibility to explain to the public how basic research leads to new medical treatments. We must explain that not every research project will lead to the development of a new medicine and that we cannot predict where the next breakthrough in science will come from. We must further make it clear to the public and lawmakers alike that to ensure that breakthroughs continue to occur, we must keep funding a broad range of basic research at a healthy level and accept that not every discovery will have an immediate impact on our lives. Alexander Fleming did not wake up one morning and decide to save human kind from bacterial infections. He made an accidental discovery (whose importance he realized) that basically allowed humans to escape natural selection. This was no small feat and arguably the most important medical breakthrough of all time.

What are you hoping to accomplish in the next few years? My lab has a long-standing interest in the cell cycle. We study the mechanisms that ensure that chromosomes are segregated accurately and what happens to cells in which these mechanisms fail, causing them to become aneuploid. While over the years we have obtained a reasonably detailed understanding of the mechanisms governing chromosome segregation we are only beginning to understand how aneuploidy impacts cell and organismal physiology. Understanding the complex impact of changing the dosage of hundreds if not thousands of genes at once is challenging, but exciting. Aneuploidy's impact on human health — it is associated with cancer and causes miscarriages and developmental defects — is also a question we are very interested in. Answering these questions will keep us busy for years to come.

But I am also always looking for new challenges. In fact, I make an effort to start a new research project every five years or so. So in this spirit we have recently begun to study mitochondria and how they communicate with the nucleus. I like a good mystery and it seems to me that there is a lot to be learned there, both from a cell biological and evolutionary perspective.

Koch Institute for Integrative Cancer Research, Massachusetts Institute of Technology, Howard Hughes Medical Institute, 500 Main Street, 76-561, Cambridge, MA 02139, USA.
E-mail: angelika@mit.edu

Quick guide

Burying beetles

Nick J. Royle, Paul E. Hopwood, and Megan L. Head

What are they? Burying beetles are members of the coleopteran family Silphidae (the carrion beetles) of the genus *Nicrophorus*. There are approximately 75 species in this Northern hemisphere genus. As for most other silphids, the use of vertebrate carrion is an essential part of a burying beetles life. But unlike other silphids, which use carrion primarily as an adult food source or somewhere to lay eggs, *Nicrophorus* beetles bury the carcasses. This 'grave-digging' behaviour gives them their common English name: Sexton beetles.

Why do they bury carcasses? This behaviour has long been a source of fascination for naturalists. The flamboyant 19^{th} century entomologist Jean-Henri Fabre, for example, devoted two chapters of his book *The Wonders of Instinct* to burying beetles: "The burying beetle...so different from the cadaveric mob in dress and habits.....across his wing-cases he wears a double, scalloped scarf of vermilion. An elegant, almost sumptuous costume....as befits your undertaker's man." The burying beetles aren't laying the bodies to rest though; instead, as Fabre explained, "he buries it in order to establish his progeny therein."

So the carcasses are nurseries for rearing baby burying beetles? Yes.

But apart from 19th century naturalists who cares about burying beetles? Burying beetles have an important role as nutrient recyclers in ecosystems and forensic pathologists like to find some species in corpses because they are bio-indicators of time of death, but it is behavioural and evolutionary ecologists that care most about burying beetles. Apart from other burying beetles that is.

Why is that then? In addition to being particularly well-dressed

Figure 1. Wild female *Nicrophorus vespilloides* feeding well-developed larvae. (Photo: Paul Hopwood.)

burying beetles are also very fine parents. Not only that but they are unusually flexible in their parental care in response to changes in their environment. This makes them ideal subjects for studying the evolution of parental care and cooperation and conflict over reproduction.

What is special about their parental care? Extended parental care in invertebrates is relatively rare, and where it exists it is usually basic (guarding eggs, for example). But burying beetles have complex parental care that resembles that provided by birds feeding dependent offspring.

Burying beetle parents feed their young….. so what do they do exactly? *Nicrophorus vespilloides* is the most common species in Europe and the one we know most about. They can bury corpses that weigh up to 500 times as much as themselves, in only a few hours (equivalent to a human burying a beached whale by hand, before breakfast). Once buried, the carcass is rolled into a ball, stripped of its fur or feathers and the female lays eggs in the soil nearby. Both beetles form a brood chamber, known as the 'crypt', in which they embalm the carcass using anal and oral anti-microbial secretions to slow putrefaction. The larvae hatch, some two to three days after the eggs are laid and, crawling to a bowl-shaped crater on the prepared carcass, they meet their parents and enjoy their first meal; a soup of partially-digested carrion.

The larvae can feed directly on the prepared carcass, but they do even better (grow faster) when fed by their parents. The beetle larvae beg to be fed and the parents respond by regurgitating food, just like blackbirds or robins. Unlike birds, however, the begging is mostly tactile, with larvae rearing up to touch the parents with their legs (Figures 1,2). Parents continue to provide care for several days before their interest in the larvae wanes and the adults depart (males typically before females), leaving the larvae to wander off to find a suitable place to pupate.

So both parents provide care? Yes. This aspect of their behaviour did not go unnoticed by Fabre either, who noted that "these grave-diggers, in truth, are remarkable fathers. They have nothing of the happy-go-lucky paternal carelessness that is the general rule among insects…". Burying beetles are particularly unusual for invertebrates (and even the majority of vertebrates) in that males provide significant amounts of care for the young. Not only that, but the form of parental care provided to offspring is extremely flexible. That is, both parents often provide care (biparental care), but males and, more typically, females will also raise their young alone (uniparental care). Moreover, although males and females often have quite distinct sex roles when providing care in a pair, with females providing most of the direct care (feeding of larvae) and males doing most of the indirect care (carcass maintenance, for example), both sexes can and do perform all parental care tasks, especially when caring alone. This flexibility in the form of care provided and the tasks performed by males and females is extremely unusual, otherwise occurring most notably in humans.

Why has such complex parental care evolved in burying beetles but not other invertebrates? Good question. Leaving aside eusocial species, such as ants, bees and termites, which have highly developed social behaviours, live in colonies and have different castes of individuals, burying beetle parental care is about as sophisticated and as flexible as it gets. The resources they use for breeding — small vertebrate carcasses — are clearly important in shaping burying beetle life-histories. Carrion is a resource with high nutritional value, making it attractive to a variety of scavengers not just burying beetles. Burial of the carrion underground reduces competition, but this doesn't in itself explain why they have such complex care. After all lots of other species of invertebrates that don't have extended parental care utilise carrion to breed. However, small vertebrate carcasses are defendable, non-renewable resources that are also rare and difficult to find. Intense competition over such a resource may have provided the necessary conditions to kick start the evolution of parental care by providing incentive for parents to stick around and guard the brood.

Once parents began to associate with their offspring, this would set the stage for the co-evolution of parent–offspring behaviours — behaviours that enhance communication between parents and their offspring — which would be favoured by natural selection if these behaviours increase reproductive success. Such co-evolution may lead to rapid diversification and complexity of parental care traits. Complex care is difficult to lose once it has evolved, because the social environment provided by family members becomes an integral component of development and reproduction.

That's all very well but why do male burying beetles stick around to provide care? Across species, male care is much more variable than female care and it is still not entirely clear why. In the majority of species with parental care females are the main care-givers. Parental care is costly. Time spent providing care is time that could be spent seeking other mating opportunities. Providing parental care may also reduce the opportunity for future reproduction

Figure 2. Wild male *Nicrophorus vespillo* feeding larvae.
Note the phoretic mites that are clinging to the male's back. (Photo: Paul Hopwood.)

too: being a parent is risky and uses up a lot of energy. Parental care can be particularly costly for males. Multiple mating with males by females means that males typically have lower probability of parentage than females. As a result males are generally expected to provide more parental care when offspring in the brood are more likely to be theirs. In other words, when males are more assured of their paternity they are more likely to provide parental care.

For burying beetles, however, the reality is slightly more complex. Experiments show that males do respond to greater paternity assurance by increasing their parental care, but only if they are young and they have a chance of breeding again: old males are better fathers and care less about female infidelity. Females provide more care than males and compensate for changes in male behaviour, increasing care when with young, insecure males and decreasing care when with old males, so reproductive success is not affected by how males respond to their assurance of paternity. As a result, the probability of parentage is not likely to be an important variable in explaining patterns of male care in burying beetles (and perhaps, other taxonomic groups too).

So if probability of parentage is not likely to be that important what is? The benefits of seeking greener reproductive pastures elsewhere are likely to depend largely on how difficult it is to gain such mating opportunities. This will depend upon things like the operational sex ratio (the ratio of sexually available males to females), the availability of carcasses for breeding and the amount of competition for these carcasses. For example, if it is hard to find new females or new carcasses to breed on, males may be better off providing parental care to protect their current brood than seeking new breeding opportunities. Paradoxically, when there is high competition among males for females and breeding resources this might actually intensify sexual selection, increasing the benefits of investing in mating over parental care for highly competitive males. It is possible that the unusual complexity and flexibility of sex roles in parental care and mating strategies in burying beetles may be largely explained by inter-relationships between the unpredictability in the availability of the carcasses they need for breeding and dynamic variation in the social environments that they experience. However, these ideas need testing.

How can these ideas be tested? Unlike with most vertebrates that have extended parental care, it is possible to study burying beetles in the wild and in the more controlled environment of the lab. In addition, their rapid generation times mean that it is relatively easy to apply experimental evolution in the lab, selecting on key traits of interest to see how patterns of parental care evolve. Burying beetle behaviour can also be filmed remotely in the wild and in the lab, and the availability of the resources they need to breed (small vertebrate carcasses) can be manipulated independent of the social environment they experience. This opens up exciting opportunities to understand how sex roles in parental care evolve in response to ecology (the availability of critical resources for breeding), and, more generally, how parental care can facilitate adaptive, plastic responses of organisms to rapid changes in their environment.

Where can I find out more?

Benowitz, K.M., Head, M.L., Williams, C.A., Moore, A.J., and Royle, N.J. (2013). Male age mediates reproductive investment and response to paternity assurance. Proc. R. Soc. Lond. B *280,* 20131124.
Eggert, A-K., and Müller, J.K. (1997). Biparental care and social evolution in burying beetles: lessons from the larder. In The Evolution of Social Behavior in Insects and Arachnids, J.C. Choe and B.J. Crespi, eds. (Cambridge: Cambridge University Press).
Fabre, J-H. (1918). The Wonders of Instinct. (London: Fisher Unwin).
Royle, N.J., Smiseth, P.T., and Kölliker, M., eds. (2012). The Evolution of Parental Care. (Oxford: Oxford University Press).
Scott, M.P. (1998). The ecology and behavior of burying beetles. Annu. Rev. Entomol. *43,* 595–618.
Trumbo, S.T. (2012). Patterns of parental care in invertebrates. In The Evolution of Parental Care, N.J. Royle, P.T. Smiseth and M. Kölliker, eds. (Oxford: Oxford University Press) pp. 81–100.
Walling, C.A., Stamper, C.E., Smiseth, P.T., and Moore, A.J. (2008). The quantitative genetics of sex differences in parenting. Proc. Natl. Acad. Sci. USA *105,* 18430–18435.

Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Cornwall Campus, Penryn, TR10 9EZ, UK.
E-mail: N.J.Royle@exeter.ac.uk

Primer

Bird brood parasitism

Martin Stevens

For many animals, the effort to rear their young is considerable. In birds, this often includes building nests, incubating eggs, feeding the chicks, and protecting them from predators. Perhaps for this reason, about 1% of birds (around 100 species) save themselves the effort and cheat instead. They are obligate brood parasites, laying their eggs in the nests of other species and leaving the hosts or foster parents to rear the foreign chicks for them. Some birds also cheat on individuals of the same species (intraspecific brood parasitism). Intraspecific brood parasitism has been reported in around 200 species, but is likely to be higher, as it can often only be detected by genetic analyses.

Currently, research suggests that obligate interspecific brood parasitism arose seven times independently during evolution. This includes three origins among cuckoos, and then one origin each in cowbirds, honeyguides, estrildid finches, and a South American duck. Brood parasites are often used as model systems for investigating evolutionary arms races and coevolution in the wild. A common scenario is that, during the course of evolution, a brood parasite begins to target a new host species, with the parasitized individuals suffering costs. Then, hosts evolve an ability to recognise foreign eggs and remove them from the nest, followed by the parasite evolving mimicry of host eggs to evade detection, hosts with improved rejection abilities, and so on. Note, however, that this simplistic scenario does not neatly fit many species that have been studied. Furthermore, what we observe in many systems seems to reflect different evolutionary stages that hosts and parasites are at, as well as entirely different trajectories of coevolution.

Until recently, much of what we knew about brood parasites was based primarily on a relatively small