5. Wright, S.I., Kalisz, S., and Slotte, T. (2013). Evolutionary consequences of self-fertilization in plants. Proc. Biol. Sci. *280*, 20130133.

6. Guo, H., Halitschke, R., Wielsch, N., Gase, K., and Baldwin, I.T. (2019). Mate selection in self-compatible wild tobacco results from coordinated variation in homologous self-incompatibility genes. Curr. Biol. *29*, 2020–2030.e5.

7. Bernasconi, G., Ashman, T.L., Birkhead, T.R., Bishop, J.D., Grossniklaus, U., Kubli, E., Marshall, D.L., Schmid, B., Skogsmyr, I., Snook, R.R., *et al*. (2004). Evolutionary ecology of the prezygotic stage. Science *303*, 971–975.

8. Firman, R.C., Gasparini, C., Manier, M.K., and Pizzari, T. (2017). Postmating female control: 20 years of cryptic female choice. Trends Ecol. Evol. *32*, 368–382.

9. Lee, H.S., Huang, S., and Kao, T. (1994). S proteins control rejection of incompatible pollen in Petunia inflata. Nature *367*, 560–563.

10. Murfett, J., Atherton, T.L., Mou, B., Gasser, C.S., and McClure, B.A. (1994). S-RNase expressed in transgenic Nicotiana causes S-allele-specific pollen rejection. Nature *367*, 563–566.

11. Sijacic, P., Wang, X., Skirpan, A.L., Wang, Y., Dowd, P.E., McCubbin, A.G., Huang, S., and Kao, T.H. (2004). Identification of the pollen determinant of S-RNase-mediated self-incompatibility. Nature *429*, 302–305.

12. Kubo, K., Entani, T., Takara, A., Wang, N., Fields, A.M., Hua, Z., Toyoda, M., Kawashima, S., Ando, T., Isogai, A., *et al*. (2010). Collaborative non-self recognition system in S-RNase-based self-incompatibility. Science *330*, 796–799.

13. Markova, D.N., Petersen, J.J., Yam, S.E., Corral, A., Valle, M.J., Li, W., and Chetelat, R.T. (2017). Evolutionary history of two pollen self-incompatibility factors reveals alternate routes to self-compatibility within Solanum. Am. J. Bot. *104*, 1904–1919.

14. Sime, K.R., and Baldwin, I.T. (2003). Opportunistic out-crossing in Nicotiana attenuata (Solanaceae), a predominantly self-fertilizing native tobacco. BMC Ecol. *3*, 6.

15. Bhattacharya, S., and Baldwin, I.T. (2012). The post-pollination ethylene burst and the continuation of floral advertisement are harbingers of non-random mate selection in Nicotiana attenuata. Plant. J. *71*, 587–601.

16. Marshall, D.L. (1998). Pollen donor performance can be consistent across maternal plants in wild radish (Raphanus sativus, Brassicaceae): A necessary condition for the action of sexual selection. Am. J. Bot. *85*, 1389–1397.

17. Marshall, D.L., Avritt, J.J., Shaner, M., and Saunders, R.L. (2000). Effects of pollen load size and composition on pollen donor performance in wild radish, Raphanus sativus (Brassicaceae). Am. J. Bot. *87*, 1619–1627.

18. Milinski, M. (2006). The major histocompatibility complex, sexual selection, and mate choice. Annu. Rev. Ecol. Evol. Syst. *37*, 159–186.

19. Ward, P.I. (2000). Cryptic female choice in the yellow dung fly Scathophaga stercoraria (L.). Evolution *54*, 1680–1686.

20. Yeates, S.E., Einum, S., Fleming, I.A., Megens, H.J., Stet, R.J.M., Hindar, K., Holt, W.V., Van Look, K.J.W., and Gage, M.J.G. (2009). Atlantic salmon eggs favour sperm in competition that have similar major histocompatibility alleles. Proc. R. Soc. B Biol. Sci. *276*, 559–566.

Migration: Ecosystem Services Helicoptered In

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There are some strange tales in the history of Natural History, and few more so than the story of animal migration. It took centuries to work out some of the astonishing features of bird migration: now a new study of hoverflies points out some more that occur among the insects.

In the northern hemisphere the disappearance of many types of bird in winter was suggested by Aristotle to be caused by hibernation. This belief persisted until only about two hundred years ago, and there are remnants of the idea in the oddest of places. For example, barnacle geese were supposed to hibernate as goose barnacles in the intertidal, hatching out in spring — hence the names. Swallows were supposed to hibernate in the mud at the bottom of ponds, and their experience with mud was the reason for collecting it to make their nests in the summer. Today we are used to the idea of bird migration, and its spectacular scales of distance and number. Arctic terns move from their Arctic breeding grounds to the Antarctic each year; radar observations have shown the huge scale of Europe-wide migration by small birds [1,2], and dataloggers regularly track individual birds all the way between, say, Africa and the UK.

What about insects? Again we are now accustomed to think of insects such as desert locusts or monarch butterflies migrating during part of their life-cycle, and again radar has demonstrated the huge scale and massive numbers involved in, for example, moths migrating into the UK in spring and back again in autumn [3,4]. Of course, unlike birds, there are no repeat migrations for any individual insect: any return migration involves a different generation. But just as in birds, this behaviour has been shown to bring substantial reproductive benefits, in

Figure 1. The marmalade fly (*Episyrphus balteatus*).
The hoverfly is feeding from a *Convolvulus* flower (photo: H. French).

Figure 2. Direction of hoverfly migration in late summer across Europe.
The directions of movements in the autumn of hoverflies across Europe, as recorded haphazardly in the literature during the 20th century. Adapted from a figure created by Pierre Goeldlin in 1981, and subsequently published by Torp [15].

the noctuid silver Y moth *Autographa gamma*, for example [3]. Attaching micro-transmitters to dragonflies and other large insects has also shown the great scale of their movements [5]. A new study by Wotton *et al.* [6] reported in a recent issue of *Current Biology* extends such data to hoverflies (Diptera: Syrphidae). Even more than birds, insects (and hoverflies) appear and disappear at different times of the year, and again the obvious hypothesis is that they overwinter as immatures, to reappear again the following year. And in fact that is exactly what does happen in the vast majority of cases. However, there are many exceptions, including among the hoverflies.

In August 1864, George Symes concluded that one hoverfly (*Scaeva pyrastri*) must be migratory because a boat at sea was enveloped in huge swarms, and the beaches and waves of Dorset were covered with thousands of dead ones [7]. A century of scattered casual observations followed from all over Europe, mostly of a handful of species including *Episyrphus balteatus* (the marmalade fly, Figure 1), always in late summer and autumn, and always with a preponderance of females with undeveloped ovaries. A Swiss team set up a huge net in the alpine passes at Col de Bretolet every year between 1962 and 1973 for four months between July and September, catching 2.4 million syrphids pouring over the pass into Italy [8]. More than half of them were *Episyrphus balteatus*. There was, therefore, no doubt about the huge scale of autumn migrants moving southwards in Europe (Figure 2). But what about a spring return?

In many of the books and papers about hoverflies, the marmalade fly is stated to overwinter in the UK as an adult, unlike many other species that overwinter either as larvae or pupae. This is because a few adult females can be found out on warm days in early spring, and have clearly overwintered. But we now know from laboratory experiments that this species cannot survive most European winters, with zero survival at -5, 0 or even 5 °C [9], and as some had long suspected [10], annual invasions must take place from the south. Since this species is by far the commonest hoverfly in the UK, with its aphid-feeding larva and flower-visiting adult, the implications of these invasions could be substantial.

Enter the era of radar research on insects! Previous studies have documented the massive scale of insect migration in both spring and autumn, perhaps 1,000 tonnes of biomass, mostly moving during the day [11]. Wotton *et al.* used a 10-year dataset of radar recordings representing an area of radius 300 km of southern Britain. Obviously radar data do not tell you what species produce the detections, and so, amazingly, they were able to filter these data for the size and shape of *Episyrphus* hoverflies. The resulting numbers were closely correlated with data for hoverfly records from the Hoverfly Recording Scheme, a huge compilation of well over a million records of enthusiastic amateurs and professionals in the UK [12]. The tracks of the hoverfly radar records were North-North-West in spring and South in autumn, but random in summer, as we might expect for migrating insects. Thus the ability to select hoverflies, and aphid-feeding ones in particular, from the radar information is convincing.

Now comes the innovative bit. With such data, the authors then calculated the scale and impact of these migrants on the ecosystem services of pollination (by adults) and aphid biocontrol (by the resulting larvae). No one has ever been able to put numbers to these services before, and they are truly staggering. They calculate that an average of 2.6 billion hoverflies fly over the Channel every year, ten times more than the estimated numbers of *Autographa* moths, and 70 times greater than the largest recorded number of painted lady butterflies. 20%

arrive in spring to produce 1–2 local generations of hoverflies that are split almost equally between midsummer (40%) and autumn (40%). This is the equivalent of 380 *Episyrphus* for every hectare of land in the southern UK.

Such enormous numbers move serious amounts of nutrients into the UK: 30–80 tonnes of biomass, 1,000–2,500 kg of nitrogen, 100–250 kg of phosphorus and 50–150 GJ of energy. They also consume serious numbers of aphids during development. We have many estimates of how many each larva can consume, which of course varies with aphid size and species, and only about 2% of these larvae survive to emerge as adults but have, of course, still eaten many aphids before dying themselves. Reasonable guesstimates of these numbers leads to a total figure of 6.3 trillion aphids eaten by the first generation of hoverflies derived from the spring migrants, an average of 900,000 aphids eaten per hectare. *Episyrphus* is a particularly important predator of cereal aphids, and Wotton *et al.* estimate that it eats about 20% of the cereal aphids present in the crops in early summer.

If this wasn't enough, the migrants carry about 10–11 pollen grains of 1–3 plant species each when flying into the UK, and hence in spring transport 3–8 billion pollen grains into southern Britain, and 3–19 billion back out again in autumn.

The actual numbers for these estimates may be even larger because the radar data come from heights between 150 and 1,200 m above ground level. Insects are unlikely to fly higher than 1,200 m because it is too cold, but there may be more of them flying below 150 m.

True migrants like *Episyrphus*, which are rather few among the hoverflies, make a stark contrast with other species. Migrants appear tailor-made to be able to respond flexibly to the challenges of climate change. Just what is it that makes them different from sedentary species that can only shift their ranges very slowly through colonisation at the range margins? A very rare hoverfly such as the golden hoverfly, *Callicera spinolae*, may have colonised successfully only once, and now only survives by establishing a new population just before the old one dies out [13]. The hornet-mimicking hoverfly *Volucella zonaria* was an extremely rare vagrant to southern Britain before 1940, occasionally breeding but always dying out again. Then it established itself, and now has spread widely throughout the south and the Midlands but has taken 60 years to do so [14]. While all the time, vast numbers of their relatives arrived unseen every year by migrating high above them.

REFERENCES

1. Shamoun-Baranes, J., Alves, J.A., Bauer, S., Dokter, A.M., Hüppop, O., Koistinen, J., Leijnse, H., Liechti, F., van Gasteren, H., and Chapman, J.W. (2014). Continental-scale radar monitoring of the aerial movements of animals. Movem. Ecol. *2*, 1–6.
2. Nilsson, C., Dokter, A.M., Verlinden, L., Shamoun-Baranes, J., Schmid, B., Desmet, P., Bauer, S., Chapman, J., Alves, J.A., Stepanian, P.M., *et al*. (2019). Europe-wide patterns of nocturnal avian migration from weather radar data. Ecogr. *42*, 876–886.
3. Chapman, J.W., Bell, J.R., Burgin, L.E., Reynolds, D.R., Pettersson, L.B., Hill, J.K., Bonsall, M.B., and Thomas, J.A. (2012). Seasonal migration to high latitudes results in major reproductive benefits in an insect. Proc. Nat. Acad. Sci. USA *109*, 14924–14929.
4. Holland, R.A., Wikelski, M., and Wilcove, D.S. (2006). How and why do insects migrate? Science *313*, 794–796.
5. Kissling, D.W., Pattemore, D.E., and Hagen, M. (2013). Challenges and prospects in the telemetry of insects. Biol. Rev. *89*, 511–530.
6. Wotton, K.R., Gao, B., Menz, M.H.M., Morris, R.K.A., Ball, S.G., Lim, K.S., Reynolds, D.R., Hu, G., and Chapman, J.W. (2019). Mass seasonal migrations of hoverflies provide extensive pollination and crop protection services. Curr. Biol. *29*, 2167–2173.e5.
7. Symes, G. (1864). Swarm of *Syrphus pyrastri* on the coast near Bridport, Dorset. Zool *22*, 9273.
8. Aubert, J., Aubert, J.-J., and Goeldlin, P. (1976). Douze ans de captures systématiques de Syrphides (Diptères) au col de Bretolet (Alpes valaisannes) [Twelve years of systematic trapping of syrphids (Diptera) at the Bretolet pass (Valais Alps)]. Mitt. schweiz. ent. Ges *49*, 115–142.
9. Hart, A.J., and Bale, J.S. (1997). Cold tolerance of the aphid predator *Episyrphus balteatus*. Physiol. Ent. *22*, 332–338.
10. van der Goot, V.S. (1979). *Eristalis tenax* (Linnaeus) en *Episyrphus balteatus* (de Geer) (Dipt, Syrphidae) elk jaar als trekkers vanuit het zuiden ? [*Eristalis tenax* and *Episyrphus balteatus* as migrants from the south every year?]. Ent. Ber *39*, 34.
11. Hu, G., Lim, K.S., Horvitz, N., Clark, S.J., Reynolds, D.R., Sapir, N., and Chapman, J.W. (2016). Mass seasonal bioflows of high-flying insect migrants. Science *354*, 1584–1587.
12. www.hoverfly.org.uk.
13. Rotheray, G.E. (2004). Autecology and conservation of *Callicera spinolae*, the Golden hoverfly. English Nature Res. Rep. *581*, 1–40.
14. Morris, R.K.A., and Ball, S.G. (2004). Sixty years of *Volucella zonaria* (Poda) in Britain. Br. J. Ent. & Nat. Hist. *17*, 217–227.
15. Torp, E. (1984). Danmarks Svirrefluer [The Danish hoverflies] (Copenhagen: Fauna Books).

Cerebellar Function: Multiple Topographic Maps of Visual Space

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New evidence from the Human Connectome Project has revealed multiple maps of visual space in human cerebellum. While some features of these maps adhere to the topographic organizational principles shared among the multiple maps in cerebral cortex, some properties appear idiosyncratic.

A human being's thoughts, actions, and emotions are supported by a brain containing about 85 billion nerve cells [1]. To the layperson, and even perhaps to many cognitive neuroscientists studying the cerebral cortex, it may come as a surprise