

history traits [10]. In vertebrates, individual fitness is often measured as an absolute value, such as the lifetime reproductive success [11]. Lifetime reproductive success, however, is not an age-specific measure and thus not suitable for analysing senescence. In most studies performed so far, age-specific survival has been used as a proxy for annual individual fitness to analyse actuarial senescence. However, a possible trade-off between survival and reproduction may confound the interpretation of actuarial senescence in terms of fitness. Decreased survival with age could indeed correspond to an absence of senescence if the reproductive output increases with age at the same time, as expected under the evolutionary hypothesis of 'terminal investment' [12]. This hypothesis states that the reproductive effort of females should increase in populations in which the expected number of offspring a female produces until its death decreases with the female's age. In their analysis, Wilson *et al.* [3] used a measure of annual fitness that combines survival and reproduction [13] thus accounting for possible trade-offs. This measure is based on the relative contribution of a given individual to the population growth in a given year. By accounting for environmental variations, these individual contributions to the population growth offer a promising metric for studying senescence in free-ranging populations.

Senescence as a Life-History Process
Hamilton [14] showed that senescence should occur as an inevitable consequence of repeated reproductive events that through age-specific mutations should lead to reduced

fitness with age in any age-structured population. Both simulations of life-history tactics [15] and empirical studies on fishes [16], birds [7], and large mammalian herbivores [8] supported the contention of a pervasive occurrence of senescence in vertebrates. Kirkwood and Holliday [17] provided a life-history context for the evolution of senescence, the disposable soma theory, that is basically grounded in the energy allocation principle and involves a trade-off between longevity and reproduction. Despite such a strong theoretical context, and some case studies that have provided empirical support of this theory [18], the genetic basis required for such an evolutionary process remains undiscovered. By showing that additive genetic variance in annual relative contributions of individuals to population growth was highest in the oldest age classes of both red deer and Soay sheep living in free-ranging conditions, Wilson *et al.* [3] established a strong link between observations and theory. Whether a genetic basis generally underlies senescence in annual fitness among vertebrates, providing thereby a direct support for evolutionary theories of aging, deserves clearly further investigation.

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Insect Behaviour: Learning for the Future

Recent studies show that what, when and how a parasitic wasp learns is tailored to its specific ecological niche.

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Parasitic wasps specializing on particular hosts have evolved elaborate patterns of behaviour to breach their host's evasion strategies. Several

recent studies [1–4] emphasise that smart adaptations of the learning behaviour of some of these wasps contribute to their success as parasites. The first set of studies [1,2] concerns locality learning in a parasitic

wasp, which oviposits in butterfly eggs and learns the location of its host's eggs well before the eggs are mature enough to be exploited. The second set [3,4] examines subtle difference in the long-term memories of two closely related parasites that help these wasps adjust to their host's particular lifestyle.

Many bees and wasps learn the landmarks defining a place during elaborately choreographed flights (for example [5]). Such flights are seen in solitary wasps when they first leave their own nest — a valued resource that

they have dug and will later provision for their young. Some parasitic wasps will perform similar flights to learn the location of a potential resource that is not yet in a state to be exploited, as Rosenheim [6] described two decades ago. He discovered that such locality learning plays a major role in the interactions between the digger wasp, *Ammophila dysmica*, and the wasp *Argochrysis armilla*, which parasitizes the caterpillars that *Ammophila* has brought to provision its nest. The nest is only vulnerable to parasitism when *Ammophila* returns with a caterpillar, and has inserted it into the nest. *Ammophila* then lays a single egg and seals the nest. Thereafter the nest is safe. This provisioning period is so short that a parasite is unlikely to discover the nest during it.

Provisioning is preceded by a long and vigorous stage of nest digging, during which wasp and nest are more easily noticed, but any egg laid then is liable to forceful expulsion. The parasite takes advantage of the opportunity afforded by nest construction and performs a locality learning flight on seeing a wasp digging. It then keeps that nest site under surveillance, in order to spot when provisioning occurs. *Ammophila*, in its turn, lessens the chances of initial detection by avoiding digging during midday periods of high parasite activity [7]. Evidence that *Argochrysis* learns the site comes from placing artificial landmarks around the nest prior to the locality flight. The parasite will later search for the nest relative to those landmarks when they are shifted [6].

The pressure of parasitism on solitary wasps is so high, that it is thought to have led to the evolution of *Ammophila*'s mode of nest construction from an earlier state in which nests are excavated only after provisions have been brought to the site [8]. The temporal separation between nest excavation and later provisioning means that both host and parasite rely on locality learning to bridge the gap. Rosenheim [7] found that the monitoring of a particular nest by a parasite drops over a few days and the longer the interval that *Ammophila* leaves between the construction of the nest and its provisioning, the less is the danger of parasitism.

Van Nouhuys and collaborators [1,2] have recently discovered a similar system in another parasitic wasp, *Hyposoter horticola*. This wasp learns

the location of clusters of checkerspot butterfly eggs that can only be successfully parasitized for the few hours in which the hosts have developed into first instar larvae, but have not yet broken out of the egg. The wasps are so efficient at finding clusters in this brief period that almost all clusters get parasitized. They use the same strategy as *Argochrysis*. A wasp learns where eggs are ahead of time and then monitors their progress. Van Nouhuys and Ehrnsten [1] recorded individual wasps visiting new egg clusters and then revisiting the same clusters for up to three weeks until some eggs in the cluster had ripened. Once a wasp detects a cluster with some eggs in the right stage of maturity, it oviposits in the mature eggs and, when finished, deposits a chemical marker, deterring itself and others from parasitizing that cluster again [1]. Almost all egg clusters suffer partial, rather than complete, depredation [9].

Although self-deposited odour cues are important close-up, they do not seem to be significant as long-range navigational aids. Van Nouhuys and Kaartinen [2] observed wasps visit plants, which were in pots and so could easily be moved or exchanged. Plants with egg clusters that had already been found by wasps were replaced by fresh plants with egg clusters that wasps had never visited. The fresh plants were visited as often as plants that had not been replaced, indicating that the wasps do not deposit substances that make the plants easier to find. Cues of this kind are, in any case, likely to be counter-productive by attracting competing individuals. On the other hand, wasps are helped by having the plants in a fixed location. Plants with egg clusters were either left in a constant position, or they were displaced just before the eggs were vulnerable. About 80% of the plants in a constant position were parasitized compared with less than 40% when the plant was shifted.

To show that wasps do learn the locality of immature clusters and that they are not guided there each time *de novo* by chemical signals in the eggs or host-plants, individual wasps were tested in an outdoor enclosure where they encountered a row of plants, on one of which was an egg cluster [2]. The infected plant was marked with two cylinders. Either the plant was flanked on each side by a cylinder, or a pair

of cylinders was placed to one side of the plant. After the cluster had been visited by a wasp, the landmarks were displaced in the same arrangement about another plant, and the wasp's subsequent visits monitored. Wasps searched both in the site defined by the cylinders and in the original site, indicating that the egg's location was remembered relative to both the cylinders and to other landmarks.

The locality learning of the two parasitic wasps is an essential component of a long, sequential process leading to successful oviposition. It occurs when the insect first discovers evidence of a possible future resource and it helps secure later benefits when that resource matures. But wasps use the acquired information much sooner, for returning to and reconnoitring the nest or egg mass. The proximate function of locality learning is thus the same as it is in the conventional learning flights of bees and wasps. The difference is that the learning flights of the parasitic wasps are performed to mark a place with potential resources that are not yet in a state to have value. In contrast, the learning flights of honeybees reflect directly the value of the resources that the bees find, and their flights on leaving a sucrose feeder are longer, the more concentrated is the sucrose that it contains [10].

It is tempting when watching the smart behaviour of one's favourite animal to ascribe to it more cognitive complexity than is necessary. Although the behaviour of parasitic wasps could be described in terms of anticipation and future planning, it can equally well be explained in terms of a sequence of behaviour in which the information acquired during one component of the sequence aids the performance of later components.

Another set of recent studies by Bleeker, Smid and their collaborators [3,4] is concerned with two parasitic wasps, *Cotesia glomerata* and *Cotesia rubecula*, and species differences in the parasites' long-term memories of plant odours. The establishment of long-term memories to a rewarding stimulus usually requires several spaced trials. Gradual learning over multiple trials allows an animal to filter out noise and so reduce the risk of acquiring unreliable information. Single trial learning can occur if there is no doubt about the importance or reliability of the information to be

acquired. Single trial learning of this kind occurs in the two *Cotesia* wasps, but in different ways that may be related to the lifestyles of their hosts.

C. glomerata mostly parasitizes caterpillars of the large cabbage white butterfly, *Pieris brassica*, and lays 20 to 30 eggs in each caterpillar (Figure 1). *P. brassica* makes the job easy for the wasp by laying large clusters of eggs on a few plants within a stand, so that if a wasp encounters one caterpillar, it is almost certain to find more caterpillars close by on the same plant or on other plants of the same species. Plants damaged by herbivores often emit chemical signals, which attract predators that will attack the herbivore. Thus, when a wasp oviposits in a caterpillar feeding on a plant, the associated plant odour can be learnt as a reliable signal to the presence of other caterpillars. The wasp's initial discovery of a caterpillar is helped by its innate attraction to the odour of damaged Brussels sprouts, a common host of *P. brassica*. But the butterfly will also lay eggs on other Brassicaceae, such as nasturtium and red cabbage, and *C. glomerata* will also learn to approach the odours of these plants.

In these studies [3,4], the wasp was shown to acquire a long-lasting memory of nasturtium odour during one conditioning trial, when it oviposits once in a single caterpillar in the presence of the odour. This one trial memory, as measured by an attractive response to nasturtium odour, persists undiminished over at least five days. When measured in preference tests of nasturtium over Brussels sprout odour, the preference for nasturtium odour is initially strong, but wanes gradually after a day or so, and by four days the smell of Brussels sprout has reasserted itself.

In the experiments by Smid and collaborators [4], translation or transcription inhibitors of protein synthesis were given before a wasp was conditioned to nasturtium odour. After this treatment, *C. glomerata* showed no preference for nasturtium over Brussels sprout odour 24 hours later, whether wasps were given one or three, massed or spaced conditioning trials, indicating that the rapid establishment of the wasp's long-term memory requires protein synthesis. The preference for nasturtium was present one hour after conditioning, showing that the treatment does not interfere with initial acquisition. But it



Figure 1. The wasp *Cotesia glomerata* ovipositing in a *Pieris brassica* caterpillar. Photograph courtesy of Hans M. Smid.

was absent after four hours, suggesting that consolidation of the long-term memory is normally complete within this period.

These experiments suggest that *C. glomerata* focuses strongly on the odour associated with its first successful oviposition and develops a long-lasting, protein-synthesis-dependent memory which leads to a persistent preference for that odour. This memory will normally be reinforced during subsequent oviposition events, and it decays after several days if it is not.

The same experiments performed on *C. rubecula* gave rather different results [3,4]. This wasp specializes on the small cabbage white, *P. rapae*, which has egg laying habits that reduce its parasite load. The butterfly lays single eggs on widely spaced individual Brassicaceae plants of different species, so that when a wasp finds one caterpillar there is no guarantee of another caterpillar nearby, or that it will be on the same food plant. Odour experienced during egg-laying is not a good predictor of future success. Nonetheless, the wasp should still learn as many likely plant odours as possible so that it can be attracted to any plant likely to harbour the appropriate caterpillar. Moreover, signals from different plants of the same family most

likely carry common components. One might expect therefore that odour learning in *C. rubecula* will also be fast, but broader than that of *C. glomerata*.

As with *C. glomerata*, a single exposure to nasturtium odour during oviposition does increase *C. rubecula*'s flight reaction to the odour over several days. But *C. rubecula* requires three spaced conditioning trials before it expresses a preference for nasturtium over Brussels sprout, rather than the one that suffices for *C. glomerata* (see also [11]). In other words, although it learns odours rapidly, the learning of one odour does not immediately suppress the wasp's response to another odour, so allowing it to search for its host over a wide spectrum of odours.

The effect of protein inhibitors given before learning was much more gradual than in *C. glomerata*, even when the dosage was increased. No effect of the inhibitor was seen after four hours, and at 24 hours the preference for nasturtium was only reduced a little by the drug. The preference relative to wasps not given inhibitors dropped further over the next two days. *C. rubecula* seems to have a protein-synthesis-independent form of memory that persists for more than a day, and the wasp is slower than *C. glomerata* to engage its protein

synthesis dependent long-term memory. Further work is needed to discover whether the different forms of memory suggested by these results might be expressed in different brain areas that mediate the focused and broad responses of the two wasps to acquired odours.

These species differences show that weighing the predictive value of an odour signal, which could potentially be estimated cognitively by an individual counting its successes and failures, is instead the result of experience across many generations. It has been incorporated into species differences in learning behaviour, such that the long-term memory of an odour generates a strong preference for that odour in species for which plant odour is a reliable predictor of a resource, whereas in species for which the immediate predictive value of a particular odour is low, odour learning is enabling rather than restrictive.

In the wasp, *Argochrysis armilla*, locality learning is triggered by the sight of a wasp digging, but oviposition is delayed until *Ammophila* returns with a caterpillar. In *Hyposoter horticola*, learning is triggered by the sight and/or taste of clumps of eggs, but oviposition waits for the eggs to present additional

cues signalling their maturity. In *Cotesia glomerata* oviposition is triggered by stimuli from the host, but learning of plant odours is induced by the act of oviposition in the presence of chemical stimuli derived from the frass or silk of the host. It seems plausible that these various cues have come to evoke learning through the control of amine release, as described in honeybees and fruitflies [12,13].

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