To maximize ρ_A, we set $a \rightarrow \infty$ and $c = 0$. For large populations, we obtain $\rho_A = [1 - w(1-b)]/[2 - w(2-b-d)]$. For $w \rightarrow 0$ we have $\rho_A = 1/2$. For $w = 1$ we have $\rho_A = b/(b+d)$. This fixation probability of A corresponds to a constant relative fitness of $1 + (b/d)$ or a net selective advantage of b/d. Hence there can be enormous selection pressure for replacement of a strict Nash equilibrium in arbitrarily large, finite populations (when the other equilibrium is much more efficient).

The calculation here uses the fact that from state $i = 1$ the system can go either to $i = 0$ or $i = 2$. Because $a \rightarrow \infty$ and $c = 0$, fixation of strategy A is certain from state $i = 2$. Hence, the fixation probability from $i = 1$ to $i = N$ is just the probability $P_{12}/(P_{12} + P_{10}) = (1 - w + wb)/(1 - w + wb + 1 - w + wd(N-2)/(N-1))$. This holds for all w. For large N, we obtain the above formula for ρ_A.

Risk dominance

Let ρ_A denote the probability that a single A player reaches fixation in a population of B. Let ρ_B denote the probability that a single B player reaches fixation in a population of A. We obtain:

$$\frac{\rho_A}{\rho_B} = \prod_{i=1}^{N-1} \frac{f_i}{g_i} \qquad (3)$$

For weak selection (small w) we find $\rho_A/\rho_B = 1 + w[(N/2)(a + b - c - d) + d - a]$. It follows that $\rho_A > \rho_B$ is equivalent to $(N-2)(a-d) > N(c-b)$. For large N this means $a - c > d - b$. Hence, if both A and B strategies are strict Nash equilibria then the risk-dominant equilibrium has a higher fixation probability when starting from a single player using that strategy. For general N and w, risk-dominance does not decide whether ρ_A is greater than ρ_B.

More general strategies

We have mostly studied the dynamics between AllD and TFT. The repeated Prisoner's Dilemma, like other repeated games, admits a huge set of possible strategies, which makes it difficult to explicitly analyse the dynamics of evolution. In general, a strategy for playing the repeated Prisoner's Dilemma is a mapping from any history of the game between two players into the interval [0, 1], denoting the probability of cooperation on the next move. However, we note that for the finitely repeated game, AllD is a strict Nash equilibrium in comparison with all cooperative strategies, where we define a 'cooperative strategy' as a strategy which cooperates on the first move. Let us divide cooperative strategies into two subsets: (1) those that are dominated by AllD and (2) those that are bistable with AllD. In an infinitely large population, no cooperative strategy can ever invade AllD. In a finite population of size N, strategies of the second subset can invade and replace AllD provided inequality (2) holds and selection is sufficiently weak.

In an infinitely repeated Prisoner's Dilemma with time-average payoffs, it turns out that TFT dominates AllD. In this case it can be shown that the 'win-stay, lose-shift'[30] strategy (also known as 'Pavlov' or 'perfect tit-for-tat') is the only simple strategy which cannot be invaded by any other strategy, and that it is the only strategy that is evolutionarily stable in an infinite population when actions are taken with a vanishingly small probability of error[11]. Moreover, this strategy is also the unique ESS in a model where strategies are encoded by finite-state automata, and the complexity of the automaton represents an evolutionary cost[31].

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Pre-social benefits of extended parental care

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The evolution of helping, in which some individuals forfeit their own reproduction and help others to reproduce, is a central problem in evolutionary biology. Recently proposed insurance-based mechanisms rely on a pre-existing life history with a long period of offspring dependency relative to the short life expectancies of adult carers[1–4]: a lone mother's offspring are doomed if she dies young, whereas after a helper dies, other group members can finish rearing the offspring[5,6]. A critical question, however, is how this life history could evolve in ancestral non-social populations, as offspring survival would then depend on a single, short-lived carer. Here, we resolve this paradox by focusing on the extended parental care inherent in prolonged dependency. We show experimentally that in non-social wasps, extended care can significantly reduce the impact of interspecific parasites. Under extended care, offspring are less vulnerable by the time they are exposed to parasites, and costs of parasitism are reduced because mothers have the option to terminate investment in failing offspring. By experimentally simulating aspects of extended care in a species where it is lacking, we demonstrate that neither benefit requires specialized behaviour. Such benefits could therefore offset the disadvantage of prolonged dependency in non-social species, thereby facilitating the evolution of helping.

Immature nest-building wasps are helpless larvae that are entirely dependent on adult carers for food. The duration of parental care is minimized in 'mass provisioning' wasps, including most non-social taxa[7,8]: before it even hatches from the egg, each offspring is sealed into a cell containing all of the food that it will require for maturation, so that it is nutritionally independent of its mother. In contrast, almost all eusocial and a few non-social wasps have extended parental care. These 'progressive provisioners' feed each developing larva gradually as it grows[7,8]. Whereas a single mass provisioner can fully provision about 1 offspring per day, provisioning is extended over 5–70 days in progressive provisioners[4,9,10]. Even if they provision multiple offspring simultaneously, non-social progressive provisioners will, on average, leave fewer independent offspring than mass provisioners, because mothers are more likely to die before provisioning is complete (Fig. 1). If extended parental care evolved before helping, as assumed by many models[1–4], what benefits offset this obvious disadvantage?

The non-social wasp genus *Ammophila* (Sphecidae) has long been a focus of study[11,12], and includes species with and without extended care. Females nest alone and place each offspring in a separate burrow, which is kept closed when the female is away hunting. Mothers provide paralysed caterpillars as food (Fig. 2), laying an egg on the first caterpillar at the time it is placed in the burrow. Some species mass provision one offspring at a time, sealing each burrow permanently 1–2 days after oviposition[12,13]. Other species, however, are progressive provisioners. These oviposit on the first caterpillar, but provide further food only gradually once the egg has hatched, so that provisioning is extended over 5–9 days[9,12]. During periods between feeds, progressive provisioners start off other burrows, and usually have 2–4 offspring in mid-provisioning at a time[9]. Cuckoo flies (Diptera: Miltogramminae) are major natural enemies of wasps[14–16]. They gain access to *Ammophila* burrows only while they are open during feeding events. Flies deposit live maggots that destroy the immature wasp and then eat the provisions[9,13,17].

We tested two mechanisms through which extended care might ameliorate the effects of interspecific parasitism. First, progressive provisioning might delay offspring being exposed to parasitism until they are less vulnerable. Each provisioning event represents an opportunity for parasites, but under progressive provisioning only the first event occurs before offspring enter the larval stage[14,18], whereas under mass provisioning an offspring receives all of its feeds while still an egg. In experiment 1 we tested whether larvae are better defended than eggs by challenging immature wasps of different ages with miltogrammine maggots (*Metopia*). In the progressive provisioner *Ammophila pubescens* Curtis[9], 15 out of 23 wasp eggs were destroyed by maggots, whereas wasp larvae were almost immune to attack (only 3 out of 22 failed: $\chi^2 = 10.4$, $P < 0.005$). We found that offspring of the mass provisioner *Ammophila sabulosa* (L.)[13,19] would be similarly protected were it to provision progressively: its larvae were also much more likely than eggs to survive experimental parasitism (25 out of 36 versus 2 out of 25 survived: $\chi^2 = 20.2$, $P < 0.001$). *A. sabulosa* eggs rarely hatch before provisioning is complete[13], so that larvae are unlikely to encounter fly maggots in nature—larval immunity probably results from unspecialized traits such as increased cuticular toughness.

A second possible advantage of progressive provisioning is that by investing only gradually as their offspring develop, mothers have the opportunity to intervene or terminate investment early if offspring show signs of failing[20]. By the time a progressively provisioned burrow receives its second feed, cuckoo parasites introduced with the first feed will have killed the wasp egg and begun growing. In experiment 2, we tested whether mothers can respond adaptively to growing parasites[9]. We removed egg-bearing caterpillars from *A. pubescens* field nests on the evening of oviposition (Fig. 2b) and incubated them with fly maggots in the laboratory overnight. We replaced caterpillars in their burrows before wasp activity began next morning, by which time they bore growing maggots on the collapsed wasp egg. All 16 mothers that we tested abandoned their parasitized offspring after their next visit to the nest, thus saving approximately 80% of the provisioning effort that would have been wasted on a failed offspring. In contrast, 14 out of 19 controls had further provisioned their nests by the time our observations ended ($\chi^2 = 16.7$, $P < 0.001$).

Experiment 2 showed that *A. pubescens* mothers respond adaptively to parasites, but it did not test whether their response depends on extended parental care. This would be the case if mothers were able to respond only to parasites that have grown during the delays between feeds that occur under progressive provisioning. In experiment 3 we performed this critical test using the mass provisioner *A. sabulosa*. Soon after a mother had oviposited on her first caterpillar, we removed the nest contents and either added five tiny fly maggots, leaving the wasp egg intact (treatment 1), or added one to two larger maggots and squashed the wasp egg (treatment 2). Treatment 1 is what a mass provisioner would typically encounter at a parasitized

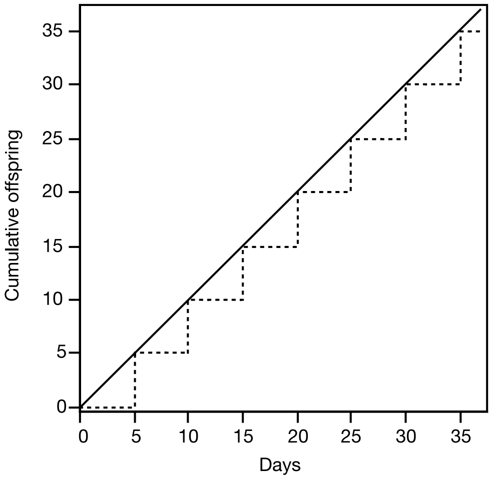

Figure 1 Offspring production under mass versus progressive provisioning. The graph shows the cumulative number of offspring fully provisioned by a non-social mass provisioner (solid line) that can fully provision one offspring per day, and by a progressive provisioner (dashed line) that uses the same food to provision batches of five offspring simultaneously over 5-day periods. On average, the mass provisioner will die with more of her past investment represented by fully provisioned offspring.

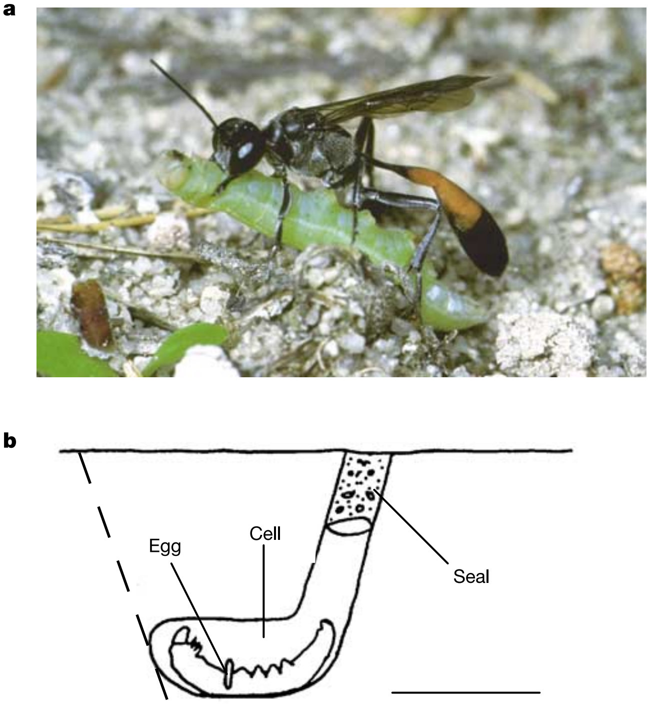

Figure 2 *Ammophila* nesting biology. **a**, *Ammophila pubescens* female carrying a paralysed caterpillar to her burrow. (Photograph by M. Blösch.) **b**, *Ammophila* burrow with first caterpillar. Soil to the left of the dashed line was excavated in experiments 2–3, allowing contents to be removed without damaging the burrow or its entrance. Scale bar, 2 cm.

nest, whereas treatment 2 mimics what *A. sabulosa* would encounter after a feeding delay at the evolutionary origin of progressive provisioning. Because *A. sabulosa* normally brings additional feeds within hours of oviposition, the maggots did not grow appreciably before the mothers encountered them on their next visit to the nest. All nine mothers exposed to tiny maggots showed no detectable response, and continued provisioning their doomed offspring to completion. In contrast, five out of twelve mothers exposed to larger maggots abandoned their burrows on the next visit, after pulling out the burrow contents (Fisher's exact $P = 0.045$). A further six of these mothers re-oviposited after pulling the manipulated caterpillar from the burrow and either discarding it, or attempting to remove fly maggots and then replace it in the burrow. Decisions to abandon appeared to be strategic: females whose burrows had contained a greater weight of food when maggots were added tended to be less likely to abandon (U-test, $P = 0.07$). The response to growing parasites may reflect periodic exposure to them during mass provisioning: at some sites up to 40% of *A. sabulosa* nests received their final feeds on the day after oviposition (J.F. and S.B., unpublished data), by which time parasites will have grown and destroyed the wasp egg.

Our results indicate how extended parental care might evolve in non-social populations, potentially facilitating the subsequent evolution of helping[1–6]. Extended care provides two complementary advantages. The first is that offspring are older, and therefore less vulnerable[21–23], when they are exposed to enemies. The second advantage is that mothers are in a position to detect mortality factors that become apparent only gradually, and can avoid wasting a full quota of investment on affected offspring. Such mortality factors[16,17] might include offspring predation, larval diseases with delayed symptoms, or fungi attacking food provisions, as well as cuckoo parasites. For a mass provisioner, however, it is too late, as females have already invested fully in their offspring by the time that such mortality becomes detectable.

Extended parental care magnifies insurance-based advantages that favour helping, and its distribution thus helps to define an important dichotomy in how sociality evolved[24]. Progressive provisioning occurs sporadically among wasps and bees, including most major groups with eusocial species[12,14,25–27]. Its absence from other groups, notably halictid bees[26], may partly reflect a constraint: the ancestral sequence of oviposition and provisioning. Both non-social and social halictids oviposit only at the end of provisioning[26], whereas progressive provisioning requires the reverse sequence. The occurrence of progressive provisioning will also depend on the balance between costs through prolonging offspring dependency versus benefits that depend on the frequency and type of mortality factors operating. High maternal mortality rates and larger numbers of offspring provisioned simultaneously will lead to increased costs (see Fig. 1). Greater prevalence of mortality factors whose effects are mitigated through progressive provisioning will lead to increased benefits. Our results show how, even at its evolutionary origin, progressive provisioning can lessen significantly the impact of cuckoo parasitism, a major source of immature mortality in key non-social taxa such as eumenine wasps, the sister group of social vespids[25,28]. Similar advantages are likely to apply for other kinds of enemy[16,17,21–23], with the possible exception of some parasitoids that attack only after provisioning is complete[16]. Progressive provisioning also facilitates the evolution of other social attributes. By prolonging contact between adult and immature wasps, it fosters larval–adult communication and nutritional interdependence[8,29]. It allows the provision of liquefied and divided prey items directly to larvae[8,25] and, in larger societies, gives helpers greater control over colony investment decisions[30]. Progressive provisioning may thus influence not only whether helping evolves, but also the eventual form taken by a society. □

Methods

Work was conducted in north Norfolk (*A. sabulosa*) and at Thursley Common, Surrey (*A. pubescens*). In experiment 1, we placed egg-bearing caterpillars from *Ammophila* field nests in natural-sized laboratory cells hollowed out in sand and covered with glass slides. Under these conditions, we obtained 100% success in rearing 10 unmanipulated offspring of each species through to the cocoon stage. Immature wasps were challenged by placing two *Metopia* maggots, freshly dissected from adult flies, 1 cm away on the caterpillar and then maintaining cells in darkness at room temperature (17–22 °C). Immature wasps were challenged at a range of ages, but eggs were mainly at 7–14 h after oviposition, and larvae within 48 h of hatching. There was no evidence that larval immunity was dependent on age. In experiment 2, control caterpillars were removed from nests and then replaced unmanipulated. In experiment 3, tiny maggots were freshly dissected from *Metopia* in the field, whereas larger maggots had been grown for 1–2 days in the laboratory. In experiment 3, nest contents were replaced within 20 min of their removal. In experiments 2–3, female wasps were individually marked and a maximum of one nest per female was used in each treatment.

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