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Evolution: How Not to Detect a Brood Parasite

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An elegant study on social parasitism in digger wasps quantifies the costs and benefits of kin recognition and shows that recognizing non-kin comes at a cost. This supports ‘Crozier’s paradox’ of why kin recognition genes are unlikely to evolve when rare alleles are selected against.

Nepotism is widespread in nature, a pattern that can be explained by kin selection. By helping a relative, an altruistic organism enhances the fitness of identical altruistic genes it shares with that relative. Kin selection is most often associated with active recognition of kin [1], suggesting that cooperative animals benefit greatly from the ability to distinguish kin from non-kin. Kin recognition is also used to avoid helping non-relatives, as occurs in social parasitism where cheaters try to reap the benefits of receiving help. A potential mechanism for kin recognition involves the matching of different alleles of a ‘recognition gene’, whereby relatives would share the same allele, but non-kin would have a different allele and be discriminated against. Such a mechanism requires a diversity of alleles in the population, which leads to an interesting conundrum, known as Crozier’s paradox [2]. According to this theory, individuals with rare recognition alleles are genetically mismatched with more individuals in the population than are individuals with

common alleles, resulting in a higher frequency of negative interactions (compared to individuals with more common alleles). The social costs that come with having rare alleles result in lower fitness for their bearers, which eliminates the very allelic diversity necessary for kin recognition genes to work.

‘Crozier’s paradox’ remains controversial, as key assumptions may be too simplistic [3–5]. Crozier’s idea is also difficult to test empirically; how does one test something that is predicted not to exist? As a result, researchers have attempted to quantify the costs of allelic rarity and the benefits of allele matching to determine whether the difference is sufficient to satisfy Crozier’s model. For example, the success of an invasive ant may be due to the high costs and subsequent loss of rare recognition alleles, which led to the loss of inter-colony aggression [6]. Now a new study in *Current Biology* by Jeremy Field and colleagues [7] directly tests for fitness costs that would be incurred from rare recognition

alleles, using a novel approach: the recognition of within-species brood parasites in a solitary ground-nesting wasp.

Ammophila wasps (Figure 1) are solitary breeders that invest heavily in offspring by providing paralyzed caterpillars for nourishment. A female *Ammophila pubescens*, the species studied by Field and colleagues [7], digs a short burrow and provisions a paralyzed caterpillar upon which she attaches one egg. A few days later the female revisits the nest for an ‘assessment visit’ to check on the hatched larva. If all is deemed well, she will continue to bring more caterpillars before finally sealing the burrow. This high investment in offspring has favored the evolution of within-species brood parasitism in many *Ammophila* species, with parasites gaining the benefits of parental care without paying the costs of provisioning. The brood parasite enters the burrow of another female after the mother has provisioned her first caterpillar and before the return assessment visit. The parasite then

removes the caterpillar and attached egg, replacing it with a different caterpillar and her own egg. While the parasite may provide no further caterpillars for her offspring, the original (host) female often continues to provision the developing parasitic larva with additional caterpillars as if it were her own offspring. An undetected parasite is very costly to the host because her investment yields zero fitness (assuming parasites are not related to the host female).

Brood parasitism is found in many insects and birds—both within and between species — and has selected for host-defense behaviors, such as recognition and rejection of parasitic offspring [8–10]. *A. pubescens* is no exception, and in ~40% of parasitized nests the host removes the caterpillar with a parasite's egg during the assessment visit, replacing it with a new caterpillar and a new egg of her own. In their study, Field and colleagues [7] address two important questions: first, would kin recognition by allele matching at 'recognition genes' be favored as a mechanism to recognize brood parasites, or does Crozier's paradox apply? Second, how do wasps that remove parasitic offspring recognize that they are not their own?

Field and colleagues [7] test an assumption implied by Crozier, namely that it takes two to tango. Digger wasps show specialized roles in each encounter — one individual is the host and the other the parasite. We might expect strong selection for the host to identify parasitic (non-kin) eggs using a recognition gene, in order to avoid the costs of raising someone else's offspring. But Field and colleagues [7] argue that Crozier's paradox will apply as long as all individuals engage in both roles (host and parasite) with equal frequency. Imagine a host that has a rare recognition allele allowing her to determine that a parasite egg (with a more common allele) is not her offspring and reject it. This same female's own parasitic offspring would similarly be rejected by most other hosts because its rare recognition allele would not match their more common recognition alleles. Therefore, if all females are equally likely to be host and parasite across their



Figure 1. A female wasp (*Ammophila pubescens*) with a paralyzed caterpillar.

Ammophila pubescens is a 'progressive provisioner' [13,16] — a female digs a burrow and lays an egg on the first caterpillar provisioned. She continues to bring additional caterpillars to the burrow to nourish the developing larva. 'Mass provisioners', in contrast, seal their egg in a burrow with all of the caterpillars their larva will consume during growth. Assessment visits, an essential prerequisite for the rejection behavior studied by Field and colleagues [7], occur only with progressive provisioning (photo: Steven Falk).

entire lives, the fitness effects from the two roles cancel out — what goes around comes around. Field and colleagues [7] provide convincing evidence that most females do indeed engage in both the host and parasite roles. An impressive 80% of the marked females that were observed in more than one reproductive interaction acted as both host and parasite. This result is similar to another study on treehoppers [11], where the majority of females exhibit both roles of host and brood parasite. However, within-species brood parasitism in well-studied bird species usually occurs at a much lower frequency [10].

Next, Field and colleagues [7] evaluated whether selection would favor the evolution of recognition genes for parasite rejection, given that females take on these roles with equal frequency. Their approach addressed a key assumption of Crozier, namely that negative interactions involving mismatched recognition alleles — in this case between host and parasite females — be sufficiently costly. Rather than directly studying allele frequencies, Field and colleagues [7]

used field data to predict whether the conditions for a Crozier effect apply to their wasps. They estimated the net payoffs for rejection and acceptance of parasite eggs based on estimates of the offspring gained or lost, combined with the known costs of parental investment. Importantly, they evaluated what the fitness payoffs for rejection and acceptance would be if the observed rejection behavior were based on a recognition gene. Here, the fitness effects of each role (host or parasite) become very important—fitness for kin recognition is calculated by summing the fitness effects for a brood parasite and for a host. If these fitness effects cancel out perfectly, then rejection (kin recognition) would be equivalent to acceptance (non-recognition). However, Field and colleagues [7] show that in digger wasps there are even greater costs to rejecting relative to acceptance—when a female rejects a parasitic egg, she also removes the caterpillar to which it is attached. Rejection would therefore force the female to replace that caterpillar, adding costs to both host and parasite roles.



Figure 2. Eggs of American coots (*Fulica americana*).

There is considerable variation among females in egg shape, background color and markings. American coots can distinguish their own eggs from those of brood parasites, using some of these egg features.

When summed across both the host and parasite roles (which are equally frequent in this species) the conditions for Crozier's paradox are met. Thus, there is selection against the use of recognition alleles generally, but because individuals with rare alleles would be involved in a higher frequency of rejections, selection would be strongest against rare alleles.

These fitness calculations indicate that rejection of brood parasites in *Ammophila* should not be based on genetic cues, a prediction further supported by two elegant experiments. Field and colleagues [7] transplanted eggs between nests, to control for all cues but genetic ones, and found that hosts did not reject these foreign eggs. This rules out the use of genetic cues and points to a non-genetic cue. As parasite eggs are typically laid a day or two after the host's egg, the inevitable age difference between host and parasite offspring could lead to hosts detecting that the egg or larva is significantly younger than expected. Field and colleagues [7] found that hosts do indeed use this information — females rejected over 50% of the younger experimental parasitic offspring added to their nest but none of the same aged offspring. The ability to detect these smaller larvae may have evolved

via the fine-tuned abilities of *Ammophila* to detect the offspring of other parasitic insect species, such as 'cuckoo' wasps or 'cuckoo' flies [12,13].

Crozier's paradox might also be relevant to other reproductive contexts. Male birds providing offspring care do not seem to be able to recognize which chicks in their nest are sired by other males [14,15]. Various explanations have been proposed for this puzzle [14,15], but one possibility is that males are equally likely to sire extra-pair offspring (i.e. benefit from non-recognition) as to raise the offspring of another male. If so, the fitness costs and benefits of recognition would cancel out the same way as in the wasps. Within-species brood parasitism is also common in some birds, and the parallels with brood parasitism in insects have been noted previously [8]; might they also share a Crozier effect [9]? Like *Ammophila* wasps, some birds recognize and reject parasitic eggs [9,10] and in many species, egg features vary considerably among females (Figure 2). It is tempting to conclude that these egg features evolved as egg recognition signatures to combat within-species parasitism, but if individual females are both host and parasite, the fitness benefits of distinctive eggs could cancel out across roles [9]. If a Crozier effect applied to

birds the findings of Field and colleagues [7] might extend well beyond *Ammophila* wasps.

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