Infanticidal male eresid spiders

SIR — The reproductive interests of males and females rarely coincide, being most polarized when the parental effort of each sex is highly asymmetrical, for example when females alone care for the brood.

Males may prevail in sexual conflicts even to the extent of forcing their interests on females1. Probably, the costliest male strategy to a brood-caring female is infanticide, where a male kills her offspring. So far, male infanticide is known only in mammals2 and birds1. We have found male infanticide (ocicide) in a spider species in which the females exhibit extreme maternal care: Segestria siciliana (Eresidae) females provide suicidal care to the matriarchal hatchlings of her single clutch. Thus, once having produced eggs, a female does not benefit from further matings. But a male that fights with a female and wins will remove the egg sac, forcing the female to replace her clutch.

Spiders have provided dramatic examples of sexual conflict in which the male loses by being cannibalized after, during or even before mating4. Males are frequently at a disadvantage because they are generally smaller than females5. However, the eresid spider S. siciliana provides an example of a sexual conflict in which females lose despite their size advantage. Female S. siciliana usually produce only one egg sac, although they can lay replacement clutches if it is removed (J.M.S. and Y.L., manuscript in preparation). The young cannot leave the egg sac on their own; even after their mother releases them from the cocoon they depend on her completely for food and protection during the two weeks after hatching5. The female always dies in the course of brood care because the young kill and consume her two to three weeks after hatching. Thus, females make a terminal investment of all their resources in caring for a single clutch, whereas males contribute no parental care (see ref. 9).

We studied a natural population of 278 female spiders with egg sacs on the Avedat plateau in the central Negev desert, Israel, of which 63 (22.7%) lost their first clutch. Males were responsible for the loss of the egg sacs in 33% of these cases. In S. siciliana, the mating and egg-laying seasons overlap, such that late-maturing males are still searching for females when up to 50% of the females already have egg sacs (Fig. 1). Loss of the egg sac is costly to a female; therefore, it is not surprising that females defend them aggressively against males.

In field tests, we placed males of known size and reproductive history at the edges of webs of females guarding egg sacs. Females succeeded in chasing males off their webs in 28 (51%) of 55 experimental contexts. Males sustained injuries in 3 (5.5%) instances. A male that succeeded in entering the tube-like nest of a female guarding her egg sac used his chelicerae — appendages modified as pincer-like jaws — to remove the threads that attach the egg sac to the inner wall of the nest. Then, he manoeuvred the egg sac to the nest entrance and eventually dropped it to the ground. Once the egg sac was removed, the female could not retrieve it.

What do males gain from infanticidal behaviour? We determined the mating success of males, individually marked at maturation, by checking all female nests for male presence (Fig. 2). Using presence in females' nests as an indication of mating success, we estimated that a male can expect to encounter and mate with an average of 1.2 females. Thus, if a searching male encounters a female with an egg sac and does not mate with her, he is likely to lose most of his expected mating success.

In entelegyne spiders such as the Eresidae, the female's sperm-storage organ (spermatheca) has separate ducts for insemination and fertilization6. Spermathecal morphology suggests that the sperm of the first male to mate with a female will have priority in fertilizing her eggs6. Furthermore, clutches of S. siciliana are small (40–140 eggs); sperm depletion is unlikely because we have observed that females produce viable second egg sacs without additional mating. In such a case of first-male sperm priority and no sperm depletion, an infanticidal male could expect little fertilization success.

We examined the sperm priority pattern...
in S. lineatus using a sterile-male technique, in which irradiated sperm competes with normal sperm for 'fertilizing' eggs, but after 'fertilization' no embryo develops. By irradiating males with 15 krad \( \gamma \)-radiation from a \( ^{240}\)Co \( \gamma \)-emitter (Department of Nuclear Engineering, Ben Gurion University), sperm were made sterile without affecting male performance. Females were paired with two males in all combinations of normal (N) and sterile (S) males: NN (n = 13 from the previous year), SS (n = 10), SN (n = 14) and NS (n = 10). None of the eggs in the SS matings hatched. We corrected the hatching success of clutches from NS and SN matings by the proportion of unhatched eggs in the NN controls (13.6%). There was no first-male priority. Indeed, the calculated probabilities of fertilization by first (P1) and second (P2) males to mate suggest a complete mixing of sperm: P1(NN) = 0.417, P1(NS) = 0.607, P2(SN) = 0.583 and P2(NS) = 0.393. Sterile sperm had a slightly lower fertilization probability than normal sperm, but this was the case regardless of whether the first or the second male was sterile.

Controlling sperm mixing in the spermatheca means that a male can expect a similar fertilization success in matings with females with or without eggs. The adaptive value of male infanticide in these spiders is that males increase their reproductive success at the expense of males that matured earlier in the season, although at a cost to the females. For males, infanticide is always advantageous because their reproductive success increases with the number of matings, which is perhaps the only option for late-maturing males. But there is a risk. For females that lose their clutch to an infanticidal male, there are costs of lower survival and reduced fecundity (our unpublished data). Also, the offspring of females that escape a replacement clutch disperse late in the season and have less time to grow before the abundance of flying insects decreases. Smaller juveniles have a lower probability of survival. This may also be a cost for the male which is expressed in the reduced fitness of his offspring. However, a male that matures late in the season will have late-dispersing offspring regardless of whether he mates with a female with eggs or a virgin female.

Infanticidal males of the spider S. lineatus gain matings, but decrease female survival and fecundity. This male behaviour can persist only if the costs to the male's offspring are smaller than the direct benefits to him. Male infanticide has not been observed previously in spiders, nor to our knowledge in other invertebrates. However, sexually selected infanticide may be more common than previously recognized. We predict that male infanticidal strategies will be found in more invertebrate species that exhibit extreme maternal brood care.

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**Protein–RNA molecular recognition**

Sir — The non-canonical G•U wobble pair is an important secondary structural feature of several RNA helices. Although connected by two hydrogen bonds, G•U differs in its geometry from a Watson–Crick base pair. It participates in both protein–RNA and RNA–RNA interactions. The G•U pair found in the acceptor helix of Escherichia coli alanyl-tRNA synthetase, by introducing a helical distortion. This result challenges previous in vitro studies which concluded that the role of the G•U base pair in tRNA\(_{\text{Ala}}\) is to allow alanyl-tRNA synthetase to recognize directly the 2-amino and 2'-hydroxyl groups in the minor groove of the A-form RNA helix. But, based on recent studies into the recognition of tRNA\(_{\text{Ala}}\) by E. coli glutaminyl-tRNA synthetase, we suggest that this discrepancy can be reconciled by considering the diverse in vivo and in vitro conditions in these two studies.

The in vitro studies, which involved quantification of the alanyl-tRNA synthetase of G•U, were performed at a subsaturating concentration of alanine (22 \( \mu \)M; Michaelis constant, \( K_m = 240 \mu \)M; ref. 5) due to inherent limitations of the assay system. Subsequent analysis of these experiments assumed that the use of diverse RNA substrates would not affect the kinetic parameters of alanyl-tRNA synthetase for alanine. But this critical assumption may not be valid, as it has now been shown for the glutaminyl- and tryptophanyl-tRNA synthetases that the mutation of certain nucleotides in the tRNA leads to substantial changes in the kinetic parameters of these synthetases with respect, not only to the tRNA, but also to the amino-acid substrate. The replacement of G3+C70 by G•U in the acceptor helix of tRNA\(_{\text{Ala}}\), for example, leads to an almost threefold increase in the \( K_m \) for glutamine but no significant change in the catalytic constant, \( k_{cat} \). If a comparable situation were to exist during the recognition of tRNA\(_{\text{Ala}}\) variants by alanyl-tRNA synthetase, use of a uniform subsaturating concentration of alanine would lead to non-uniform underestimation of \( k_{cat} \) and consequently to the misassignment of energetic contributions to binding.

In contrast, the in vivo assay of this protein–RNA interaction is less susceptible to such errors, because the concentration of alanine in the amino-acid pool of E. coli is almost an order of magnitude higher than used in vitro (168 \( \mu \)M; ref. 7). Nevertheless, the in vivo assay also suffers from a limitation in that the concentration of alanyl-tRNA synthetase may depend on several metabolic parameters, leading to the possibility that the observed differences in tRNA alanylation may be due to changes in the level of the enzyme itself, rather than changes in the structure of tRNA\(_{\text{Ala}}\). Add to this the possibility that alanyl-tRNA synthetase undergoes tRNA-dependent changes in its kinetic parameters for alanine, and what initially seem to be contradictory results on the recognition of G•U by alanyl-tRNA synthetase can, in fact, be readily reconciled. In this way, a nucleotide replacement that substantially reduces the level of tRNA charging under certain conditions in vitro may be effectively compensated for in vivo by increased concentrations of both amino acid and synthetase, particularly when the gene encoding alanyl-tRNA synthetase is overexpressed.

Although the problem in interpreting these results raises the perennial concern of the validity of comparing in vitro and in vivo approaches to studying molecular recognition, it shows that in this case the question of direct or indirect recognition will finally be resolved only by determining the crystallographic structure of tRNA\(_{\text{Ala}}\) complexed with alanyl-tRNA synthetase.

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