



When are neighbours ‘dear enemies’ and when are they not? The responses of territorial male variegated pupfish, *Cyprinodon variegatus*, to neighbours, strangers and heterospecifics

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Dear enemy recognition reduces the costs of territorial defence in some species, but not others, when a neighbour is more threatening to a resident's fitness than an intruder. I asked whether dear enemy effects were fixed in a particular species, or if the reduced aggression between a resident and neighbour was disrupted by the presence of potential mating opportunities. Observing variegated pupfish, *Cyprinodon variegatus*, in the field and in the laboratory, I examined the effects of a female's presence in a male's territory on residents' aggressive responses to conspecific neighbours and strangers as well as heterospecific opponents. Although reduced aggression consistent with dear enemy recognition was seen between conspecific neighbours in the absence of females, the presence of a female in a male's territory instigated comparably greater aggression between the neighbours. No reduction in aggression was seen between pupfish males and heterospecific opponents. These findings suggest that dear enemy recognition may be a flexible, rather than a fixed, feature of the relationship of neighbouring conspecific males. Despite the disruption in dear enemy recognition caused by a female, residents in the laboratory faced with neighbours spent more time associating with the female than residents faced with strangers. This allowed the residents to secure as many spawns as did males who had been faced with no competitor. Residents faced with any other type of opponent had reduced reproductive success, suggesting that the dear enemy relationship between residents and neighbours is more complex than simply a reduction in aggression.

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Although territorial neighbours should represent one another's foremost competitors (Alexander 1974; Getty 1987), neighbouring residents often direct less aggression towards each other than towards nonterritorial intruders (Wilson 1975). This phenomenon of diminished aggression to stable neighbours relative to intruding strangers is termed ‘dear enemy’ recognition (Fisher 1954) and has been observed in a number of territorial species, including mammals (e.g. Barash 1974), amphibians (e.g. Jaeger 1981), birds (e.g. Armstrong 1991), reptiles (e.g. Qualls & Jaeger 1991), fish (e.g. Leiser & Itzkowitz 1999) and insects (e.g. Pfennig & Reeve 1989).

One hypothesis proposed to explain the occurrence of dear enemy recognition has emphasized the relative threats that neighbours versus strangers pose to a territorial resident (Temeles 1994). Consistent with theoretical game models (e.g. Maynard Smith & Parker 1976; Maynard Smith 1982), this hypothesis predicts that a

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resident should invest more in aggression against a more threatening individual that is capable of inflicting greater losses on the resident (Getty 1987). Presumably, prolonged, escalated aggression should not occur between neighbours inasmuch as neighbours, that already possess territories, are not threatening to each other's territorial resources (Wilson 1975; Jaeger 1981). Contrastingly, nonterritorial intruders are often relentlessly attacked by residents (Parker 1974; Riechert 1979; Enquist & Leimar 1987; Stamps & Krishnan 1997), because intruders may be threatening as potential usurpers of territorial space (Getty 1981, 1987).

The relative threats of neighbours versus strangers also appear to explain circumstances under which dear enemy recognition does not occur. When neighbours are more threatening than strangers to a resident, the resident should not show diminished aggression towards neighbours compared with strangers. For example, Temeles (1989, 1990) found that territorial northern harriers, *Circus cyaneus*, are more aggressive to neighbours than to floaters because floaters intrude to steal food, whereas