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## Dear Enemy Effect

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### Synonyms

[Dear enemy phenomenon](#); [Neighbor-stranger discrimination](#)

### Definition

Reduced aggression between established territorial neighbors relative to strangers

### Introduction

Territorial animals defend resources needed for survival and reproduction. Animals advertise their ownership of territories through conspicuous signals; birds and frogs vocalize, mammals and salamanders scent mark, lizards display colorful patterns, and fiddler crabs wave their oversized claws in the air. If advertisement is not enough, animals may have to fight off intruders to maintain territory ownership. However, animal fights are

relatively rare, even when territories are spatially clumped resulting in frequent interactions between neighbors. Once territories are established, individuals in neighboring territories typically respect territorial boundaries and withhold aggression from their neighbors. This makes sense because aggression can be costly, and if a neighbor already has a territory, they might not represent a threat to a territory holder. However, territory holders will often maintain a readiness to be aggressive toward unfamiliar individuals, showing more aggression to strangers than to familiar neighbors. This phenomenon of reduced aggression between established neighbors relative to strangers is called the “dear enemy effect” and is thought to allow animals to minimize the costs of territory defense (Wilson 1975).

The term “dear enemy” originates with observations made by James Fisher (1954) that songbirds often establish territories in clusters and have relationships with their neighbors that are not strictly competitive. Fisher wrote that “the effect of the holding of territory . . . is to create “neighbourhoods” of individuals which are masters of their own definite and limited property, but which are bound firmly, and *socially*, to their next door neighbours by what in human terms would be described as a dear enemy or rival friend situation.” Much of the early research on the dear enemy effect was conducted on territorial songbirds, which often respond less aggressively to the

familiar songs of their neighbors than they do to the unfamiliar songs of strangers. Since this early work on birds, the dear enemy effect has been documented in many different taxonomic groups, including insects, crustaceans, fish, amphibians, reptiles, and mammals.

## Adaptive Significance

Individuals must balance the benefits and costs of defending a territory. The primary benefit of holding a territory is the exclusive access to resources that may be limited in the environment. Defended resources may include feeding grounds, areas to advertise to and court mates, reproductive resources such as oviposition or nesting sites, and shelter. However, aggressively defending these resources from conspecifics incurs costs, such as energy spent on aggressive encounters, missed opportunities to feed or mate, risk of injury during fights, and decreased vigilance against predators. We should generally expect that evolution has equipped territorial animals with decision rules that allow them to maximize the difference between the benefits and costs of territory defense. The dear enemy effect is the product of such a decision rule, but why, exactly, is it adaptive to treat neighbors and strangers differently?

There are two hypotheses to explain the adaptive value of behaviorally discriminating between neighbors and strangers. The “relative threat” hypothesis (Getty 1987) rests on the assumption that strangers pose a greater threat to territory holders than do neighbors. The idea is that strangers are likely to be non-territorial “floaters” that are looking to establish a territory by taking over an existing territory or inserting themselves into a network of territories. Territory holders thus risk either losing their territory to a stranger or gaining an additional competitor if a stranger settles nearby. In contrast, a neighbor already has a territory of its own; neighbors may compete for mates or food but they do not pose a threat to territory ownership. By maintaining high levels of aggression toward strangers and tolerating nearby neighbors, territorial animals can both reap the benefits of possessing a limited resource

and minimize the costs of defending that resource. Along a different line of reasoning, Ydenberg et al. (1988) proposed that a dear enemy effect functions to minimize the costs of escalated conflicts between neighbors and is possible because familiar neighbors have established dominance relationships. This “familiarity” hypothesis rests on the assumption that the relationship between neighbors is established through repeated conflicts, and once dominance relationships are established, individuals are less likely to make role mistakes in future conflicts. Strangers, however, do not have established relationships and need to escalate conflicts to determine dominance roles. Thus, interactions are more likely to escalate to higher levels of aggression between unfamiliar individuals than they are between familiar neighbors.

While the “relative threat” and “familiarity” hypotheses are not mutually exclusive, they do make different predictions about when a dear enemy effect should be adaptive. The “familiarity” hypothesis predicts a dear enemy effect any time neighbors can become familiar with each other. The “relative threat” hypothesis predicts a dear enemy effect only for situations in which strangers pose a greater threat than neighbors, regardless of how familiar neighbors may be. Temeles (1994) reviewed studies of the dear enemy effect and found that the results are generally consistent with the “relative threat” hypothesis. Among birds, the dear enemy effect is typically observed in species that defend multi-purpose breeding territories, where neighbors may compete for mates or food, but strangers threaten complete territory takeover. It is often not observed in species that defend single-purpose feeding territories or nest sites, where neighbors and strangers both represent equivalent threats to food or nesting resources and are treated the same by territory holders. Some of the best evidence for the relative threat hypothesis actually comes from situations in which neighbors are more of a threat than strangers, and territory holders correspondingly direct more aggression toward neighbors (Temeles 1994).

## Neighbor Recognition

Many researchers are interested in the dear enemy effect because it allows them to study social recognition. Learning to recognize familiar neighbors allows territorial animals to direct aggression toward strangers, producing a dear enemy effect. However, the dear enemy effect and neighbor recognition are not synonymous. A dear enemy effect could be produced in the absence of neighbor recognition. For example, if individuals that do not possess territories behave differently than individuals that have territories, the behavioral cues of non-territorial strangers could be perceived as more threatening and elicit stronger aggressive responses from territory holders. On the other hand, one could observe neighbor recognition in the absence of a dear enemy effect if, for example, territory holders are more aggressive toward neighbors than strangers. Finally, a lack of observed behavioral discrimination between neighbors and strangers cannot rule out the possibility that a territory holder recognizes a neighbor but simply treats neighbors and strangers with equal levels of aggression.

Nevertheless, many studies of the dear enemy effect are also tests of neighbor recognition. The pioneering work on neighbor recognition was conducted on songbirds (Stoddard 1996). Territorial male songbirds often respond more aggressively to the songs of strangers than the songs of neighbors played from the direction of the neighbor's territory, showing that they learn to recognize the vocalizations of their neighbors. Further, territory holders often respond more aggressively to their neighbor's songs played from an unfamiliar location than from their neighbor's territory, suggesting that these birds have the capacity to recognize multiple individual neighbors based on vocalizations and location (Stoddard 1996). Similar results have been obtained in territorial bullfrogs (Bee et al. 2016) and damselfish (Myberg and Riggio 1985). Some studies have demonstrated individual recognition of neighbors independent of location. For example, though male bullfrogs are more aggressive to the vocalizations of a neighbor played from an unfamiliar location,

they still show less aggression to neighbors in an unfamiliar location than to strangers in an unfamiliar location (Bee and Gerhardt 2002). Another experimental approach uses a neutral arena; Husak and Fox (2003) showed that male collared lizards are less aggressive toward familiar neighbors in the field and in staged interactions in a neutral arena, demonstrating individual recognition independent of location.

The dear enemy effect has allowed researchers to investigate a variety of perceptual and learning mechanisms that allow animals to recognize familiar individuals. In order to recognize familiar neighbors, territorial animals must be able to perceive the differences in signals produced by different individuals. Experiments in sparrows and bullfrogs have shown that territorial individuals can perceive individual differences in frequency of vocalizations, allowing them to recognize the vocalizations of familiar neighbors (Brooks and Falls 1975; Bee et al. 2016). Research on the dear enemy effect has also revealed that territorial animals can learn to recognize familiar neighbors through habituation, a common form of learning in which animals gradually decrease response to a stimulus with repeated exposure to that stimulus. Neighbors may initially be aggressive with each other during territory formation, but their aggression gradually habituates as territory boundaries are established. Because habituation is specific to a certain stimulus, habituation to the signal properties of a familiar neighbor can allow a territory holder to recognize a particular individual by those signal properties (Bee et al. 2016). Other forms of learning are certainly involved in neighbor recognition in some species. For example, song sparrows have dear enemy relationships with their neighbors, and neighbors interact with each other by singing songs that they share in common (Beecher et al. 1996).

## Conclusions

The dear enemy effect occurs when territorial animals direct less aggression toward established territorial neighbors than toward strangers. This is a common phenomenon among territorial animals

and has been documented in many different taxonomic groups. By withholding aggression from neighbors, animals can minimize the costs of territory defense. The general consensus of research on the dear enemy effect is that animals are more aggressive to strangers because strangers pose a greater threat to territory holders than do neighbors. The dear enemy effect is often made possible by the ability to recognize familiar neighbors and has allowed researchers to understand some of the perceptual and learning mechanisms that underlie this common form of social recognition.

## Cross-References

- ▶ [Aggression](#)
- ▶ [Habituation](#)
- ▶ [Individual Recognition](#)
- ▶ [Territoriality](#)

## References

- Bee, M. A., & Gerhardt, H. C. (2002). Individual voice recognition in a territorial frog (*Rana catesbeiana*). *Proceedings of the Royal Society of London B: Biological Sciences*, 269, 1443–1448.
- Bee, M. A., Reichert, M. S., & Tumulty, J. (2016). Assessment and recognition of competitive rivals in anuran amphibians. *Advances in the Study of Behaviour*, 48, 161–249.
- Beecher, M. D., Stoddard, P. K., Campbell, S. E., & Horning, C. L. (1996). Repertoire matching between neighboring song sparrows. *Animal Behaviour*, 51, 917–923.
- Brooks, R. J., & Falls, J. B. (1975). Individual recognition by song in white-throated sparrows. III. Song features used in individual recognition. *Canadian Journal of Zoology*, 53, 1749–1761.
- Fisher, J. (1954). Evolution and bird sociality. In J. Huxley, A. C. Hardy, & E. B. Ford (Eds.), *Evolution as a process* (pp. 71–83). London: Allen & Unwin.
- Getty, T. (1987). Dear enemies and the prisoner's dilemma: Why should territorial neighbors form defensive coalitions? *American Zoologist*, 27, 327–336.
- Husak, J. F., & Fox, S. F. (2003). Adult male collared lizards, *Crotaphytus collaris*, increase aggression towards displaced neighbours. *Animal Behaviour*, 65, 391–396.
- Myberg, A. A. J., & Riggio, R. J. (1985). Acoustically mediated individual recognition by a coral reef fish (*Pomacentrus partitus*). *Animal Behaviour*, 33, 411–416.
- Stoddard, P. K. (1996). Vocal recognition of neighbors by territorial passerines. In D. E. Kroodsma & E. H. Miller (Eds.), *Ecology and evolution of acoustic communication in birds* (pp. 356–334). Ithaca: Cornell University Press.
- Temeles, E. (1994). The role of neighbours in territorial systems: When are they “dear enemies”? *Animal Behaviour*, 47, 339–350.
- Wilson, E. O. (1975). *Sociobiology: The new synthesis*. Cambridge, MA: Harvard University Press.
- Ydenberg, R. C., Giraldeau, L.-A., & Falls, J. B. (1988). Neighbours, strangers, and the asymmetric war of attrition. *Animal Behaviour*, 36, 343–347.