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The role of neighbours in territorial systems: when are they 'dear enemies'?

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Abstract. Many territorial animals respond less aggressively to neighbours than to strangers (the dear enemy phenomenon). The dear enemy phenomenon generally has been assumed to represent neighbour–stranger interactions for all territorial systems. Here studies of territoriality are reviewed and the occurrence of the dear enemy phenomenon is shown to depend on the kind of territory studied: it tends to be present in studies of multi-purpose, breeding territories, but absent in studies of feeding territories. Moreover, whether a territory owner interacts less strongly with a neighbour than with a stranger in studies of colonial nesting birds is a function of nearest nest distance. These results support hypotheses that explain the dear enemy phenomenon based upon the relative threat presented by neighbours versus strangers, but not those based upon familiarity with neighbours versus strangers. Hence, the role of neighbours may vary depending upon territorial conditions, and an owner's potential gains and losses from interactions with neighbours and strangers.

Many territorial animals respond less aggressively to intrusions by their territorial neighbours than to intrusions by non-neighbours (strangers). This difference in the intensity of territory owners' responses to neighbours and strangers has been termed the 'dear-enemy phenomenon' (sensu Fisher 1954).

Recently, I found that female northern harriers, *Circus cyaneus*, defending winter feeding territories responded more aggressively to their territorial neighbours than to non-territorial floaters (strangers); i.e. they did not exhibit the dear enemy phenomenon (Temeles 1989, 1990). Consequently, the purpose of this review was to re-examine studies of the dear enemy phenomenon in order to determine the conditions under which it does, or does not, occur.

Although the dear enemy phenomenon has been documented for a variety of animal species, its causes remain poorly understood and controversial (e.g. Ydenberg et al. 1988, 1989; Getty 1989). The dear enemy phenomenon has been assumed to occur on all types of territories (i.e. feeding, multi-purpose, breeding), and has led authors to treat neighbours as relatively neutral in analyses of territoriality (Hixon 1980; Carpenter 1987). As noted above, however, it was not observed in two recent studies (Temeles 1989, 1990).

Hypotheses

Two major groups of hypotheses have been presented to explain the dear enemy phenomenon, which differ in their emphasis on (1) the relative threat posed by neighbours and strangers versus (2) the degree of familiarity a territory owner has with a neighbour or a stranger.

Several hypotheses for the dear enemy phenomenon propose that if territory owners can learn to recognize and respect each other's territorial boundaries, they can reduce the energy expended in territorial defence and more successfully focus their defence against potential usurpers of their territories, such as non-territorial floaters (strangers; e.g. Falls 1969; Krebs 1971, 1982; Getty 1987, 1989). Expressed in terms of game-theoretic payoffs, these hypotheses suggest that owners' potential losses to floaters may be higher than their potential losses to neighbours: that is, owners may stand to lose both mates and territories to floaters, whereas they may only stand to lose mates to neighbours, because neighbours already have territories (e.g. Jaeger 1981; Getty 1987; Temeles 1990). These differences in potential losses could result in reduced fighting intensity between owners and neighbours relative to owners and floaters (Jaeger 1981; Getty 1987; Temeles 1990).

In contrast, Ydenberg et al. (1988) argued that the degree of escalation in a territorial interaction

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depends on the contestants' familiarity with each other. Presenting a hypothesis based on the asymmetric war-of-attrition model (e.g. Parker 1984), they suggested that a territory owner's familiarity with a neighbour as opposed to a stranger affects its estimate of the likelihood of role mistakes, where a role mistake is the probability that either contestant incorrectly judges its role as likely winner or loser (Parker 1984). Hence, territory owners respond less aggressively to neighbours than to strangers because owners are more familiar with their neighbours as a result of previous encounters with them, and role mistakes are less likely.

Getty (1989) also presented a hypothesis for the dear enemy phenomenon based on familiarity, in which he proposed that animals fight to learn about their opponents. According to his hypothesis, familiar neighbours fight very little because they have little to learn. On the other hand, strangers (owners versus floaters) fight more because they have to learn whether there is anything to be gained from fighting a particular opponent, not because they have made a mistake in adopting a role (Ydenberg et al. 1988).

Both hypotheses based on familiarity have been criticized either for inappropriate use of war-of-attrition models ('role mistake hypothesis') or dependency on the behaviour of intruders, rather than territory owners ('fighting to learn hypothesis'; Getty 1989; Ydenberg et al. 1989). None the less, there is a consensus that the dear enemy phenomenon can best be understood using a game theoretic approach, and that more empirical studies are required (Getty 1989; Ydenberg et al. 1989).

An additional criticism of familiarity hypotheses was that they seemed inadequate to explain cases in which the dear enemy phenomenon was not observed, i.e. the territorial harriers I studied (Temeles 1989, 1990). In these studies, neighbours interacted frequently and were in constant view of each other. I also observed that floaters intruded primarily to steal food, whereas neighbours appeared to usurp portions of owners' territories. In this respect, floaters were never observed to take over territories, whereas neighbours expanded their territories into those of owners on two occasions (Temeles 1990). Consequently, I hypothesized that in contrast to the dear enemy situation, territorial harriers responded more aggressively to neighbours than to floaters because they had more to lose from interactions with neighbours (territory and/or a prey item) than with floaters (primarily prey items). This hypothesis was supported by an analysis of responses of territorial harriers to neighbours versus floaters following short-term reductions in expected payoffs from aggression: when harriers were restricted from further feeding due to a processing constraint, they reduced their level of aggression towards competitors for individual prey items (floaters), but not towards competitors for territories (neighbours; Temeles 1989).

Predictions

In this paper I evaluate whether territory owners interact less aggressively with neighbours than with strangers, and whether the existence of neighbours as 'dear enemies' depends upon an owner's potential gains or losses from interactions with neighbours versus strangers (Temeles 1990). I predicted that the dear enemy phenomenon would tend to occur on breeding, multi-purpose territories, because on such territories an owner's potential losses to strangers may be higher (mate and territory) than its potential losses to neighbours (only mates; e.g. Jaeger 1981; Getty 1987; see above). In contrast, I predicted that the dear enemy phenomenon would not tend to occur where an owner's potential losses to neighbours may equal or exceed its potential losses to strangers. Such conditions probably occur on feeding territories because fluctuating food supplies may encourage neighbours to usurp portions of owners' territories (see Temeles 1990 and above). Moreover, I hypothesized that the dear enemy phenomenon might be absent when a territory owner cannot afford to surrender any space without incurring a substantial loss in fitness, such as when the defended area is a nest site or burrow. In addition to testing these predictions, I examine whether any particular study method is biased towards detection of the dear enemy phenomenon, and the general implications of the results for studies of territorial behaviour.

METHODS

I operationally defined the dear enemy phenomenon as a situation in which a territory owner responds less aggressively to a territorial neighbour than to a stranger. By this definition, the dear enemy phenomenon is not equivalent to neighbour–

stranger recognition because a territory owner might respond more aggressively to a familiar neighbour than to a stranger.

For inclusion in this survey I required that a study quantify a territory owner's response to neighbours relative to strangers. Such studies may involve playbacks of tape-recorded vocalizations of neighbours and strangers to territory owners, live introductions of neighbours or strangers on a territory, experiments in which neighbours or strangers are placed with a territory owner in a neutral arena, placement of models simulating a neighbour or a stranger on a territory, or direct observations of owners' behaviour towards intrusions by neighbours and strangers. Another criterion for including a study was that neighbours occupy territories adjacent to those of owners, whereas strangers (1) occupy territories at great enough distances from those of owners to render previous encounters with owners unlikely, or (2) are non-territorial floaters. By this criterion, some studies that have appeared in earlier reviews were not included in this one (e.g. Bertram 1970; Nolan 1978; Myrberg & Riggio 1985).

The earlier review by Ydenberg et al. (1988) served as a starting point for my literature search. In addition, I conducted a computer search of the Biosis Computer Data Base in behavioural biology, animal communication, and animal behaviour from 1966 to April 1992 using the following combinations of key words: 'dear enemy or individual recognition and territor', and 'neighbo or stranger and recognition'. (The abbreviated key words 'territor' and 'neighbo', rather than 'territory' or 'neighbour', were used because they allowed a simultaneous search of the literature under the key words 'territory', 'territorial', 'territoriality', 'neighbor', and 'neighbour', as well as other variations on these roots.) Finally, I searched the following major journals from 1965 to April 1992: *Animal Behaviour*, *The Auk*, *Behaviour*, *The Condor*, *Ethology (Zeitschrift für Tierpsychologie)*, *The Ibis*, and *The Wilson Bulletin* (I also searched *Behavioral Ecology and Sociobiology* from its inception in 1976 to April 1992).

I differentiated between types of territories using information provided by authors in the original sources. If an animal defended a small area around its nest, eggs, and/or young, I considered its territory to be a 'nest area' or 'nest burrow'. Such small defended areas are characteristic of many colonial seabirds and wasps. If an animal defended an area at least in part to acquire and retain a mate and/or breeding occurred on the territory, which tended to be the case for many male songbirds (e.g. great tit, *Parus major*; song sparrow, *Zonotrichia melodia*), I classified the defended area as a 'multi-purpose/breeding' territory. Lastly, if an animal defended an area either solely (e.g. northern harrier) or primarily (e.g. ants) to ensure a stable food supply, I referred to the area as a 'feeding' or 'multi-purpose/feeding' territory.

RESULTS

Sixty-six studies on 55 different species in five different taxa (birds, mammals, reptiles, amphibians and insects) met my criteria for inclusion in this survey and provided the database for all of my analyses. Fifty-five of these studies show evidence for the dear enemy phenomenon (Table I), whereas 15 do not (Tables I and II). Similar results were obtained if species, rather than studies, were analysed: the dear enemy phenomenon has been observed in 47 species (Table I), but not in 10 others (Table II). (Failure for these numbers to total 66 studies and 55 species results from some studies reporting different results for males and females.)

Inspection of the data in Tables I and II indicates a strong association between the presence or absence of the dear enemy phenomenon and the type of defended territory: the dear enemy phenomenon was observed in 39 of 39 species defending multi-purpose, breeding territories, but only in five of 10 species defending nest areas or burrows, and in one of four species defending multi-purpose, feeding territories. Pooling the data for nest area and feeding territories for analysis yielded a highly significant association between the presence or absence of the dear enemy phenomenon and territory type ($\chi^2 = 22{\cdot}0$, $df = 1$, $P < 0{\cdot}005$; chi-squared test corrected for continuity; Siegel 1956). These results support my prediction that whether a territory owner responds less aggressively to a neighbour relative to a stranger, and whether the dear enemy phenomenon is observed, depends on the type of area defended, and by inference, the relative threat presented by neighbours and strangers.

For the previous analysis, I excluded two species for which different results were reported for males and females: the red-winged blackbird, *Agelaius phoeniceus*, and the meadow vole, *Microtus*

Table I. Territorial species that exhibited the dear enemy phenomenon*

Species (subject)	Method	Source
Birds: songbirds		
Agelaius phoeniceus (males)	Playback	Yasukawa et al. 1982
Campylorhyncus nuchalis (both sexes)	Playback	Wiley & Wiley 1977
Catharus fuscescens (males)	Playback	Weary et al. 1987
Erithacus rubecula† (males)	Playback	Brémond 1968
	Playback	Hoelzel 1986
	Playback	Brindley 1991
Fringilla coelebs (males)	Playback	Pickstock & Krebs 1980
Geothlypis trichas (males)	Playback	Wunderle 1978
Icteria virens (males)	Playback	Ritchison 1988
Parus major (males)	Playback	Krebs 1971
	Playback	Järvi et al. 1977
	Playback	Falls et al. 1982
	Observation	Krebs 1982
Passerina cyanea† (males)	Playback	Belcher & Thompson 1969
	Playback	Emlen 1971
Pipilo erythrophthalumus (males)	Playback	Richards 1979
Seiurus aurocapillus (males)	Playback	Weeden & Falls 1959
Spizella pusilla (males)	Playback	Goldman 1973
Sturnella magna (males)	Playback	Falls & d'Agincourt 1981
Sturnella neglecta (males)	Playback	Falls & d'Agincourt 1981
Thryothorus ludovicianus (males)	Playback	Shy & Morton 1986
Zonotrichia albicollis (males)	Playback	Falls 1969
	Playback	Lemon & Harris 1974
	Playback	Brooks & Falls 1975
	Playback	Falls & Brooks 1975
Zonotrichia georgiana (males)	Playback	Searcy et al. 1981
Zonotrichia leucophrys (males)	Playback	Baker et al. 1981
Zonotrichia melodia (males)	Playback	Harris & Lemon 1976
	Playback	Kroodsma 1976
	Playback	Searcy et al. 1981
	Playback	Stoddard et al. 1990
Birds: non-songbirds		
Arenaria interpres (males)	Models	Whitfield 1986
Dendragapus obscurus (males)	Playback	Falls & McNicholl 1979
Lagopus mutus (males)	Observation	Brodsky & Montgomerie 1987
Larus argentatus‡ (both sexes)	Observation	J. Burger 1984
Larus marinus‡ (both sexes)	Observation	Butler & Janes-Butler 1982
Larus occidentalis‡ (males)	Observation	P. W. Ewald, unpublished data
Larus ridibundus‡ (males)	Observation	Patterson 1965
Melanerpes erythrocephalus (—)	Playback	Crusoe (in Falls 1982)
Phylidonyris nigra (males)	Observation	Armstrong 1991
Phylidonyris novaehollandiae (males)	Observation	Armstrong 1991
Porphyrio porphyrio (both sexes)	Playback	Clapperton 1987
Mammals		
Cercopithecus aethiops (both sexes)	Playback	Cheney & Seyfarth 1982
Dipodomys spectabilis (both sexes)	Playback	Randall 1984
	Neutral arena	Randall 1989
Lemur catta (males)	Olfactory	Mertl 1977
Microtus pennsylvanicus (females)	Olfactory	Ferkin 1988
Ochotona princeps† (both sexes)	Playback	Conner 1985
Peromyscus leucopus (both sexes)	Neutral arena	Vestal & Hellack 1978
Peromyscus maniculatus† (males)	Neutral arena	Healey 1967
	Neutral arena	Vestal & Hellack 1978
Procyon lotor (males)	Neutral arena	Barash 1974
Tamiasciurus hudsonicus (both sexes)	Playback	Price et al. 1990
Vulpes fulva (males)	Neutral arena	Barash 1974

Table I. Continued

Species (subject)	Method	Source
Reptiles		
Anolis carolinensis (males)	Neutral arena	Qualls & Jaeger 1991
Crotaphytus collaris (males)	Introduction	Fox & Baird 1992
Dipsosaurus dorsalis (males)	Introduction	Glinski & Krekorian 1985
Amphibians		
Plethodon cinereus (both sexes)	Neutral arena	Jaeger 1981
Rana catesbeiana (males)	Playback	Davis 1987
Insects		
*Acromyrmex octospinosus*** (colonies)	Introduction	Jutsum et al. 1979
Sphecius speciosus§ (females)	Introduction	Pfennig & Reeve 1989

*All species defended multi-purpose, breeding territories and exhibited a stronger response to strangers than to neighbours unless noted otherwise.

†Species exhibited the dear enemy phenomenon in some studies but not in others.

‡Species defended a nest area.

§Species defended a nest burrow.

**Species defended a multi-purpose/feeding territory.

Table II. Territorial species that did not exhibit the dear enemy phenomenon

Species (subject)	Territory type	Method	Source
Birds: songbirds			
*Agelaius phoeniceus** (females)	Multi-purpose/breeding	Playback	Beletsky 1983
Birds: non-songbirds			
Chionis minor† (males)	Multi-purpose/feeding	Observation	A. Burger 1980, 1984
Circus cyaneus† (females)	Feeding	Observation	Temeles 1990
*Larus atricilla** (both sexes)	Nest area	Playback	Beer 1970
Larus delawarensis† (both sexes)	Nest area	Observation	Dulude et al. 1989
Pygoscelis adeliae‡ (both sexes)	Nest area	Playback	Speirs & Davis 1991
*Rissa tridactyla** (both sexes)	Nest area	Playback	Wooller 1978
*Sula bassana** (both sexes)	Nest area	Playback	White 1971
Mammals			
Microtus pennsylvanicus† (males)	Multi-purpose/breeding	Neutral arena	Ferkin 1988
Insects			
Pogonomyrmex barbatus† (colonies)	Multi-purpose/feeding	Introduction	Gordon 1989

*Species exhibited no difference in response to neighbours versus strangers.

†Species exhibited a stronger response to neighbours than to strangers.

‡Males exhibited a stronger response to neighbours than to strangers, whereas females exhibited no difference in response to neighbours versus strangers.

pennsylvanicus. A discussion of these two species, however, is instructive for illustrating how differential threats may influence the magnitude of territory owners' responses to neighbours versus strangers. Specifically, Yasukawa et al. (1982) found that male red-winged blackbirds defending multi-purpose, breeding territories responded more aggressively to playbacks of strangers' calls than to those of neighbours' calls. This result is consistent with the hypothesis that on multi-purpose, breeding territories, a territorial male's potential losses to strangers (mate and territory) may be higher than his potential losses to neighbours (mate; see Introduction). In contrast, Beletsky (1983) observed that female red-winged blackbirds on multi-purpose, breeding territories exhibited similar responses to either strangers' or neighbours' calls. He noted that for a female red-winged blackbird, a neighbouring female presents just as much threat to her reproductive success as a non-neighbour.

Ferkin (1988) also observed differences in responses by male and female meadow voles to intruders that were associated with differences in the relative threat presented by neighbours versus strangers. In both field and laboratory experiments, female meadow voles responded more aggressively to strangers than to neighbours, whereas exactly the reverse was observed for males. Ferkin noted that in the meadow vole, females are philopatric. Hence, a neighbouring female is likely to be a close relative, and poses less of a threat than a stranger. In contrast, the reproductive success of a male meadow vole increases with the number of females he can monopolize, which in turn increases with the size of his home range. Neighbouring males compete for females within each other's ranges, and may cause pregnancy blocks, commit infanticide, and/or annex portions of territories. On the other hand, strangers are more often transient males passing through an owner's territory.

The contrasting results obtained in the two studies of ants defending multi-purpose, feeding territories (Tables I and II) also are consistent with the hypothesis that whether territorial animals respond less aggressively to neighbours as opposed to strangers depends on the relative threat presented by each kind of intruder. In the study by Jutsum et al. (1979) on *Acromyrmex octospinosus*, ants killed individuals from distant colonies (strangers), but not from near colonies (neighbours). The low incidence of fighting between local nests in the field was attributed to nests being genetically similar (Jutsum et al. 1979). In a study on *Pogonomyrmex barbatus*, however, Gordon (1989) observed a stronger response to neighbours compared with strangers. She noted that in the case of *P. barbatus*, neighbouring colonies were not close relatives: hence, a colony had more to fear from its neighbours, with whom it competes for food, than from strangers.

Colonial Nesters

Studies of multi-purpose, breeding territories and feeding territories support the predictions presented in the Introduction of this paper: owners of multi-purpose, breeding territories, but not owners of feeding territories, respond more intensely to strangers than to neighbours. Studies involving defence of nest sites or burrows, however, were inconsistent with my prediction: whereas I predicted that defenders of nest areas should behave with equal or greater intensity to neighbours than to strangers (i.e. dear enemy phenomenon absent), five studies of nest sites demonstrated the dear enemy phenomenon, and five did not (Tables I and II). In the case of the solitary wasp, *Sphecius speciosus*, studied by Pfennig & Reeve (1989), the occurrence of the dear enemy phenomenon may in part result from the fact that neighbouring wasps are more likely to be close relatives. The remaining nine studies of the dear enemy phenomenon involved defence of nest sites by colonial nesting seabirds (Tables I and II). Why should the dear enemy phenomenon be observed for some of these species, but not others?

Initially, I predicted that defenders of nest sites would respond more aggressively to neighbours than to strangers, because any loss of space might result in a substantial reduction in fitness; i.e. damage to eggs or young. Under such conditions, neighbours, rather than strangers, may represent a greater threat. Based on this reasoning, I hypothesized that the mixed results observed in testing this prediction might result from differences among these studies in the spacing of nest sites. If so, nearest nest distances of those species for which the dear enemy phenomenon was absent should be smaller than nearest nest distances of those species for which the dear enemy phenomenon was present. In accordance with this reasoning, both Myers et al. (1981) and J. Burger (1984) have suggested that neighbours may represent a greater threat than strangers to owners at high densities of territories.

To test this prediction, I compared nearest nest distances of those species for which the dear enemy phenomenon was absent and was present. Where possible, I used nearest nest distances presented by authors in their studies of the dear enemy phenomenon; I estimated mean nearest nest distance for *Larus ridibundus* from points presented in Patterson's Figure 1 (1965). Because nearest nest distances were not reported for two species, *Pygoscelis adeliae* and *Rissa tridactyla*, in the studies of the dear enemy phenomenon (Wooller 1978; Speirs & Davis 1991), I used nearest nest distances from other sources. The nearest nest distances presented by Porter (1990) for *R. tridactyla*

Table III. Nearest nest distances of colonial nesting birds*

Species	Nearest nest distance	Source
Dear enemy phenomenon present		
Larus argentatus	4·8 m (2·3–8·3 m)	J. Burger 1984
Larus marinus	6·7 m (±0·8 m)	Butler & Janes-Butler 1982
Larus occidentalis	9·0 m (3·0–17·0 m)	P. W. Ewald, unpublished data
Larus ridibundus	1·3 m (0·5–3·8 m)	Patterson 1965 (Fig. 1)
Dear enemy phenomenon absent		
Larus atricilla	1·2 m (0·9–1·5 m)	Beer 1970
Larus delawarensis	0·9 m (±0·3 m)	Dulude et al. 1986
Pygoscelis adeliae	0·7 m (0·6–0·8 m)	Penny 1968
Rissa tridactyla	0·8 m (0·3–2·5 m)	Porter 1990
Sula bassana	1·0 m (—)	White 1971

*Means, and, if reported, standard errors or ranges.

were measured at the same location and over the same dates as Wooller's study, and hence presumably approximate those of the birds studied by Wooller (1978).

As predicted, the mean nearest nest distance for species that did not show the dear enemy phenomenon was significantly shorter than that for species that did show the dear enemy phenomenon (Table III; nearest nest distance, dear enemy phenomenon absent, $\bar{X} \pm \text{SE}$: $0{\cdot}92 \pm 0{\cdot}09$, dear enemy phenomenon present: $5{\cdot}45 \pm 1{\cdot}60$; $t = 3{\cdot}63$, $df = 3$, $P = 0{\cdot}04$; data log-transformed; two sample t-test on Minitab, Ryan et al. 1985). A similar result was obtained excluding the two species (*P. adeliae* and *R. tridactyla*) for which I used nearest nest distances from other sources ($t = 3{\cdot}35$, $df = 3$, $P = 0{\cdot}04$; data log-transformed).

DISCUSSION

The results of this study indicate that whether a territory owner responds more strongly to strangers than to neighbours, and hence whether the dear enemy phenomenon is observed, depends on the type of defended area, and, in the case of colonial seabirds, nearest nest distance. These results are consistent with predictions presented in the Introduction based upon the relative threat posed by a neighbour or a stranger.

Acceptance of this interpretation of the results depends upon the ability to exclude alternative hypotheses. In particular, can hypotheses for the dear enemy phenomenon based on familiarity account for these results? An underlying assumption of the 'role mistakes' hypothesis presented by Ydenberg et al. (1988) is that a territory owner encounters a neighbour more frequently than a stranger. Because of its greater familiarity (number of encounters) with neighbours, an owner is less likely to make role mistakes in a contest, and hence such contests between neighbours result in less escalation than contests between owners and strangers. As noted elsewhere (Temeles 1990), for the 'role mistakes' hypothesis to explain greater aggression towards neighbours relative to strangers, an owner must have greater familiarity with strangers (or floaters) than with neighbours. Moreover, this greater familiarity with strangers must tend to occur on feeding territories in contrast to breeding territories, and among loosely packed rather than densely packed colonial territories. The familiarity hypothesis therefore seems less consistent with the available data (Tables I, II and III) than hypotheses based on relative threat.

Alternatively, Getty's (1989) 'fighting to learn' hypothesis can explain escalated fighting between neighbours if conditions on territories change. Under changing conditions, neighbours may fight at higher levels during renegotiations in order to acquire information about the state of their opponent. This explanation may account for the contrasting results observed between studies of the dear enemy phenomenon on multi-purpose, breeding territories, as opposed to feeding territories: food levels may be more stable on the former rather than the latter type of territories, and such stability may allow neighbours to recognize and respect each other's territorial boundaries. However, Getty's hypothesis seems inadequate to account for the relationship between the dear enemy phenomenon and nearest nest distance in seabirds (Table III), unless conditions change more frequently when nearest nest distances are small than when they are large.

Although familiarity undoubtedly influences a territory owner's behaviour towards neighbours and strangers, this survey of the literature suggests that other factors, particularly the relative threat presented by an intruding neighbour relative to an intruding stranger, may contribute to differences in the intensity of an owner's response to these two types of intruders. If familiarity has a role in determining the intensity of a territory owner's response to a neighbour versus a stranger, it probably results from an owner's ability to estimate potential gains and losses from interactions with these two types of intruders. Ydenberg et al. (1988) may have had this role for familiarity in mind when they conceived their hypothesis, and thus offered a mechanism for the dear enemy phenomenon. However, as shown here, a consideration of the relative threats presented by neighbours versus strangers is necessary to explain why territory owners sometimes respond more aggressively to neighbours than to strangers, as well as the reverse.

Observation Method

An alternative explanation for the results is that the presence or absence of the dear enemy phenomenon depends less upon relative threat or familiarity than it does upon the type of observation method used in a study. For example, the majority of studies in this paper examined breeding songbirds; virtually all of them demonstrated the dear enemy phenomenon, and all involved playback experiments (Table I). The percentage of species for which the dear enemy phenomenon was reported were similar across observation methods: 86% (25 of 29) of the species studied by playback of vocalizations, 70% (seven of 10) by direct observation, 88% (seven of eight) by arena experiments, and 80% (four of five) by live introductions (I excluded model, olfactory, and playback/observations experiments because of small sample sizes, $N=1$ for each). Pooling the observation, arena, and introduction studies for statistical comparison with the playback studies indicated no association between whether or not the dear enemy phenomenon was observed and whether or not playback experiments were used ($\chi^2=0{\cdot}147$, $df=1$, $P>0{\cdot}7$; chi-squared test corrected for continuity; Siegel 1956). Hence, whether or not the dear enemy phenomenon is observed does not depend upon the observation method used, especially playback experiments.

In addition, studies on two of the species in Table I suggest that when the dear enemy phenomenon is observed, it is consistent for a species regardless of the method used. Krebs (1971), Järvi et al. (1977), and Falls et al. (1982) found that great tits responded more aggressively to playbacks of strangers' than to neighbours' calls; Krebs (1982) also noted higher intensity responses by great tits towards strangers in an observational study. Similarly, Randall (1984, 1989) found that banner-tailed kangaroo rats *Dipodomys spectabilis* responded more strongly to strangers than to neighbours in both playback and arena experiments. These studies suggest that any given observation method, particularly a playback experiment, is not biased towards detecting the dear enemy phenomenon. However, simulated intrusions (especially using models, olfactory cues, or playbacks) differ from live intrusions, and additional studies demonstrating that responses to simulated intrusions approximate responses to live intrusions are needed.

Testing Hypotheses

The results of this study suggest that the relative threat presented by neighbours and strangers ultimately may influence the intensity of a territory owner's aggressive response. To a lesser extent, a territory owner's familiarity with these threats may be a prerequisite for treating neighbours and strangers differently. Hence, an objective for future studies should be to assess the relative importance of familiarity versus threat in determining an owner's behaviour.

One prediction stemming from familiarity hypotheses is that a territory owner's responses to neighbours should decrease in intensity over time, as the owner becomes more familiar with its neighbours (Ydenberg et al. 1988). To date, very few studies of the dear enemy phenomenon have looked at responses of territory owners to neighbours over time (e.g. Falls 1969; Temeles 1990), and more are needed. Observing that the intensity of a territory owner's response to neighbours decreases over time is not a confirmation of the familiarity hypotheses, because such an observation may also result from a decrease in the relative threat presented by neighbours as territorial borders become more established and secure. However, failure to observe a decrease in the intensity of a territory owner's response to neighbours over time certainly indicates that familiarity with neighbours per se does not ameliorate an owner's relationships with its neighbours.

In addition, my analyses suggest that studies of animals defending both nest sites and feeding territories may be useful for assessing whether the intensity of a territory owner's responses to neighbours and strangers (floaters) depends upon the relative threat presented by these two types of intruders. As shown here, whether or not a colonial nesting seabird interacts more aggressively with strangers relative to neighbours depends upon the distance to the nearest nest (Table III). This conclusion is based upon an analysis across different species, and corroboration via within-species studies is desirable. Such within-species studies may involve observations of owners' responses to neighbours and strangers as a function of nearest nest distance between birds within the same colony (e.g. comparisons between low- and high-density sites), or studies of owners' responses to neighbours and strangers before and after experimental manipulations of nearest nest distances. Owners should respond more aggressively to neighbours than to strangers when nearest nest distances are small (presumably because neighbours are a greater threat to eggs and chicks), but should respond more aggressively to strangers than to neighbours when nearest nest distances are large, possibly because strangers are more likely to be settling pairs trying to usurp portions of territories for nest sites. Analogous experiments on hummingbirds by Ewald (1985) offer some insights as to how manipulation of threats may influence aggression between neighbours. When the distance between territory centres was progressively decreased by moving artificial feeders closer together while keeping the location of the territorial border constant, neighbouring territorial hummingbirds switched from little aggression to highly escalated contests (Ewald 1985). The rate of high-intensity fighting between neighbours in these experiments was significantly higher than that against neighbours prior to moving feeders closer together or against non-neighbouring intruders during either period.

Finally, the handful of studies on feeding territories for the most part have not recorded the dear enemy phenomenon (Table II) and are consistent with my hypothesis that, on feeding territories, strangers (floaters) may intrude primarily to steal food, whereas neighbours may intrude primarily to claim additional space (Temeles 1990). One prediction suggested by this hypothesis is that an owner's relationships with neighbours and floaters on feeding territories may depend upon the quantity and stability of the food supply. This prediction could be tested by analysing the intensity of a territory owner's responses to neighbours and floaters in relation to experimental manipulations of the food supply on its territory. At low, fluctuating resource levels, neighbours may attempt to expand territories, and hence a territory owner may be predicted to respond more aggressively to its neighbours than to floaters. At high, constant resource levels, territory owners may have little need for additional space. Hence, floaters, rather than neighbours, may be the greater threat, and territory owners might be expected to respond with equal or greater intensity to floaters than to neighbours.

Conclusions

The main conclusion drawn from this study is that the dear enemy phenomenon is not a permanent fixture of all territories, but rather may vary depending upon conditions; i.e. the relative threat presented by neighbours in comparison to strangers. One could argue that the high number of studies reporting stronger responses by territory owners to strangers as opposed to neighbours indicates that the dear enemy phenomenon is the rule, and not the exception, for neighbour–stranger relationships on territories. However, most studies of the dear enemy phenomenon involved animals defending multi-purpose, breeding territories (see Tables I and II), such as male songbirds. It is likely that many of these species, especially male songbirds, were deliberately studied with the expectation of observing the dear enemy phenomenon. This bias may have led to an over-representation of studies reporting the dear enemy phenomenon in my survey.

Although my analyses indicate an association between the dear enemy phenomenon and the type of territory under study (Tables I and II), a territory owner's gains and losses from interactions with neighbours or strangers, rather than the type of territory, may be of greater significance in predicting the intensity of an owner's responses to neighbours and floaters. For example, Stoddard et al. (1990) observed the dear enemy phenomenon in a study of male song sparrows, *Zonotrichia melodia*, on multi-purpose, breeding territories. However, in a year with intense competition for territories and a high frequency of take-overs leading to unstable boundaries between neighbours, the dear enemy phenomenon was not recorded for many breeding males (Stoddard et al. 1990). None the less, the breeding territories, feeding territories and nest areas examined in this study differed in a number of ways, including size, vegetative cover, defence costs and defended resources. Further work is required to determine the extent to which these variables influence the association between type of territory and an owner's responses to neighbours versus strangers. Moreover, the association between the dear enemy phenomenon and territory type found here is based upon an analysis across different species. Comparison studies involving species that defend different territories when breeding (breeding territory) and not breeding (feeding territory) might prove useful in elucidating the factors contributing to this association.

As hypothesized here, the relative threat presented by a neighbour versus a stranger ultimately may dictate the magnitude of a territory owner's response to a neighbour versus a stranger. Although this hypothesis has been offered in one form or another by various authors over the years to explain the dear enemy phenomenon (e.g. Weeden & Falls 1959; Falls 1969; Jaeger 1981; Getty 1987; Temeles 1990), surprisingly few studies have made any attempt to determine a territory owner's potential gains and losses from interactions with neighbours versus floaters (e.g. Falls 1969; Brodsky & Montgomerie 1987; Temeles 1989, 1990). Additional studies of the relative threat presented by neighbours versus strangers are desirable. Such studies should consider differences not only in the benefits of defence against neighbours versus strangers (e.g. possession of territory, mate, or food), but also in the costs of eviction stemming from differences between neighbours and strangers in fighting ability, information, and proximity to the owner's territory. For example, neighbours can 'go right next door' when in an interaction with an owner, which might affect their threat relative to strangers by making them harder or easier to evict.

Failure to assess relative gains and losses from interactions with neighbours and floaters may result in part from the use of playback experiments to study neighbour–stranger relationships. Playback experiments, especially those performed on songbirds, typically focus on the mechanisms by which habituation to a stimulus may develop, and as a result have emphasized an owner's familiarity with neighbours' and strangers' calls, rather than the relative threat presented by these two types of intruders. However, my results indicate that a determination of a territory owner's potential gains and losses from interactions with neighbours and floaters will be necessary in order to ultimately understand the roles neighbours play in territorial systems.

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