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ORIGINAL ARTICLE

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Neighbor–stranger discrimination in Audubon's shearwater (*Puffinus l. lherminieri*) explained by a "real enemy" effect

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Abstract Neighbor–stranger discrimination (NSD) occurs when animals respond with more aggression to strangers than to territorial neighbors. NSD has been reported in many species that defend multi-purpose territories for breeding and foraging, but it is rare among species that defend other types of territories. For birds that defend only their nest sites, there is no experimental evidence for NSD, and observational studies have provided mixed results. In a colony of Audubon's shearwaters (*Puffinus l. lherminieri*), I played back the calls of a neighbor and a stranger to males defending nest sites. Subjects responded with longer calls to playbacks of strangers than to those of neighbors. In shearwater colonies, strangers are often birds looking for future breeding sites. In contrast, there is no evidence that established breeders compete with their neighbors for any resources. Shearwaters should benefit from NSD because strangers represent a "real enemy" and established neighbors do not.

Keywords Dear enemy · Neighbor–stranger discrimination · *Puffinus lherminieri* · Territoriality · Vocalization

Introduction

Territorial animals in a wide range of species respond more strongly to displays of strangers than to those of neighbors near the territorial boundary (reviewed by Temeles 1994; Stoddard 1996). A few studies have found that such neighbor–stranger discrimination (NSD) only occurs when the stimulus is presented near the correct boundary with the neighbor (Falls and Brooks 1975; Wiley and Wiley 1977; Davis 1987; Godard 1991; Stoddard et al. 1991). This result indicates that subjects learn the vocalizations and locations of individual neighbors (neighbor–neighbor discrimination NND). Subjects could learn to discriminate neighbors from strangers by habituation to the form and location of neighbors' displays or by a more complex mechanism of learning (Wiley and Wiley 1977; Richards 1979; Godard 1991; Bee and Gerhardt 2002). Regardless of the mechanism of learning used for discrimination, the difficulty of correctly assigning calls to neighbors and strangers should increase with the density of signalers and the ratio of variation within to variation among individuals (Beecher 1989; Jouventin et al. 1999; Mackin 2004).

The most frequent evolutionary explanation for both NSD and NND is the "dear enemy" effect. Fisher (1954) argued that territorial songbirds are social despite their distance from each other, because they both benefit from and have a conflict with their neighbors. In modern terms, neighbors are described as "dear enemies" because holders of territories have less conflict with each other than with strangers. By cooperating about the location of boundaries, they can focus their time and energy on other activities (Godard 1993). Although there are a number of possibilities for the evolution of cooperation (see Lotem et al. 2003), discriminating regular partners from strangers should always facilitate the evolution of cooperation between unrelated individuals (Trivers 1971). For instance, cooperation between unrelated individuals can be evolutionarily stable if they use strategies like 'tit-for-tat' to retaliate against defecting partners (Trivers 1971; Axelrod and Hamilton 1981).

For territorial neighbors, only Godard (1993) has provided experimental evidence for a strategy like "tit-for-tat." When she played a neighbor's song in the center of a male hooded warbler's (*Wilsonia citrina*) territory, the subjects reacted aggressively to that neighbor's song at the edge of the territory 1 h later. In control trials, which substituted a stranger's song in the center of the male's territory, the same subjects reacted with baseline levels of aggression to the neighbor's songs at the edge. Thus, hooded warblers

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retaliated against individual neighbors that failed to reciprocate.

Cooperation is not the only possible evolutionary explanation for NSD. If one category of signaler is more threatening than another, then discriminating between the two signalers would always be beneficial. In this case, conditional strategies would not be necessary. Potential examples include species that defend only nest sites, such as freshwater sunfish (Family Centrarchidae) and most species of seabirds, and those that defend sites for mate attraction in choruses or leks. NSD has been demonstrated experimentally for one such species. American bullfrogs (*Rana catesbeiana*) respond more aggressively towards calls by strangers (Davis 1987) and calls with unfamiliar fundamental frequencies (Bee and Gerhardt 2001a, 2001b, 2002) while defending sites for sexual advertisement and the deposition of eggs (Howard 1978a, b).

In colonial seabirds, the proximity of neighbors appears to influence interactions among them. Observational studies have suggested NSD by four species of gulls (Laridae) that nest in diffuse colonies (spacing >1 m). In contrast, other studies found no evidence for NSD by three other gulls, a penguin (Spheniscidae), and a booby (Sulidae), all of which nest in dense colonies (spacing ≤ 1 m; Temeles 1994). Four of the five studies with negative results included experimental tests (*Larus atricila*, Beer 1970; *Rissa tradactyla*, Wooller 1978; *Pygoscelis adeliae*, Speirs and Davis 1991; *Sula bassana*, White 1971). Thus, NSD might break down in dense colonies.

Such experiments that do not find NSD are difficult to interpret. In addition to no discrimination of the two categories of stimulus by the subjects, possible explanations for the negative results include a type II error in statistics (missed detection of a positive result), an inadequate design, and equal treatment of the two stimuli despite an ability to distinguish the categories (Stoddard 1996). Especially in a colony of birds, many individuals respond to a vocal stimulus, and arranging equipment for an experiment often disrupts normal behavior. In addition, visual displays that accompany vocalizations are difficult to simulate.

Nocturnal procellariiforms offer a way around these difficulties. These seabirds defend only their nest sites and use vocalizations for mate recognition, mate attraction, and nest defense (Brooke 1978; Bretagnolle 1996). Because they are nocturnal, playbacks of vocalizations can realistically simulate intrusions by neighbors or strangers. Nevertheless, relationships among neighbors have not been described within this group. In the present study, I tested whether or not Audubon's shearwaters (*Puffinus l. lherminieri*), which nest in diffuse colonies, respond differently to neighbors' and strangers' calls played near the subjects' nests.

Methods

I worked in a large colony (800–1200 pairs) of Audubon's shearwaters at Long Cay, Exuma Cays Land and Sea Park, The Bahamas (24°24.47′ N, 76°39.95′ W). Recordings were made during March (egg-laying), May (incubation/chick-rearing), and June (chick-rearing) from 1 to 3 years before the experiment (Mackin 2004). Playbacks were conducted in June 2002, at a time when active breeders foraged away from the colony during the day and returned to their nests every 1–6 nights to feed their single chicks.

It can take several years for a shearwater to obtain a nest and to attract a mate (Storey 1984; James 1985). Once the bond is formed, pairs normally breed together in the same cavity as long as both survive (Harris 1966; Perrins et al. 1973; Harris 1969). At Long Cay, estimates of adult survivorship ranged from 88 to 94% over the 5 years of the study. The birds nested in crevices in the Karst limestone with an average density of 1.97 nests per 100 m^2 (Mackin 2004). Shearwaters used almost any cavity that could fit two adults and provide shelter from rain and heat, and established breeders returned to the same cavities each year (Mackin 2004). This behavior created neighborhoods that were largely stable from year to year.

Recordings of vocalizations

These shearwaters' calls consist of 1–10 phrases. Each phrase contains 1–8 harmonic, exhalant notes and one long, hoarse, inhalant note (Mackin 2004). Individuals produce calls with different numbers of phrases and different numbers of exhalant notes in each phrase. Phrases by the same individual with the same number of notes, however, are similar in timing and acoustic frequency between years, between nights in the same year, and within nights (Fig. 1; Mackin 2004). These features of calls are probably important for individual recognition in this species and in other procellariiforms (Brooke 1978; Bretagnolle 1989, 1996; Bretagnolle and Lequette 1990; Mackin 2004).

Between 1999 and 2001, I recorded males that were countersinging with neighbors or responding to playbacks of calls by strangers. Calls were recorded with a Sony TC-D5M tape recorder and Sennheiser ME-80 directional microphone or a Sony MZ-R70 mini-disc recorder and Realistic 33-2001A omni-directional microphone. I then captured the callers, gave each bird an individually numbered leg band, took several morphological measurements, and returned them directly to their nest cavities. Only calls by males were used in the experiment, because, as in other procellariiforms, males called more frequently and performed most defense of nest cavities (James 1985; Bretagnolle 1996).

I digitized the calls with a PowerMac G4 and WildSpectra sound analysis software (Wiley and Wiley 2002). I then recorded clean, 5- to 8-s examples of calls by 14 different males onto a mini-disc. Each track consisted of the same example repeated four times with 30 s between the starts of calls, which is a short but not unnatural interval between calls. Potential differences in the salience of different examples were controlled by the experimental design (see below).

I constructed a lightweight playback system with a 2.5 W pre-amplifier wired to an 18 W bridge-tied load monaural

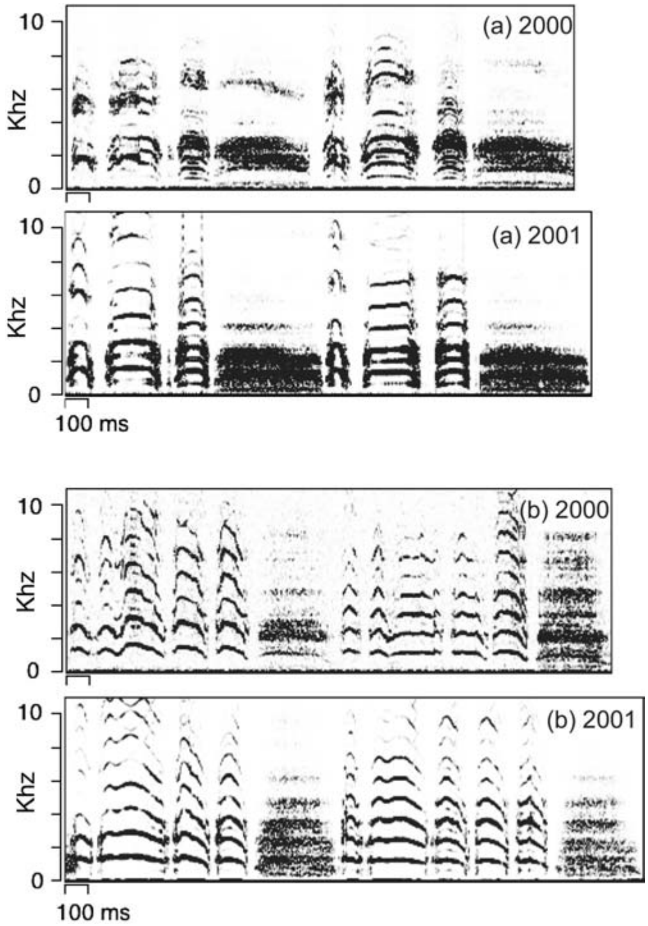


Fig. 1 Spectrographs of sections of calls by two male shearwaters (**a** and **b**) recorded in different years

amplifier (Hitachi HA 13118; frequency response = 50–20,000 Hz; 12 VDC) and a Realistic Minimus-7 speaker (40 W; nominal frequency response = 50–20,000 Hz). To the human ear, the playbacks from this system sounded like the original calls. All playbacks were within the natural level of amplitude within the population (76–80 db peak SPL at 2 m, Realistic Sound Pressure Level meter, C-weighting, fast response). In addition, recordings of playbacks showed that all paired broadcasts were within 3 dB SPL.

Procedure for playbacks

Before beginning the playbacks, I randomly paired the 14 recorded males to produce seven pairs of recordings for playback. The males in each pair had nest sites in different areas of the colony (50–400 m apart), so that each of the recorded males could simulate a neighbor in one trial and a stranger in a second trial. Each subject heard a neighbor in one playback and a stranger in the other.

Before each trial, I walked to the nest of one of a pair of recorded males and ensured that he was not present. I then chose a male subject that controlled a nest cavity within 5 m of the recorded male's nest. I placed the speaker between the recorded male's nest and the subject's nest at a distance of 0.25–0.5 m from the subject, and I directed the speaker toward the subject. I flipped a coin to decide whether the recording of the neighbor or the stranger would be played first. Each trial consisted of a 5-min period before playback, a 2-min playback of one call every 30 s, a 5- or 10-min period between the playbacks, a second 2-min playback, and a 5- or 10-min period after playback.

After this trial, I went to the nest of the second of the pair of recorded males, chose a subject for the playback in the same way as before, and played the calls back in the same order as in the previous trial. This protocol ensured that seven subjects heard a neighbor's call first and seven heard a stranger's call first. In addition, if one of the two recordings provided a more salient stimulus, any effects on responses would cancel because the more salient call would be used as a stranger in one trial and as a neighbor in the other.

I conducted trials during the darkest portion of the night (between 9:45 p.m. and 4:15 a.m.). After the first trial of a pair, I immediately attempted the complementary trial near the other recorded male's nest. In five of the seven pairs, both trials were completed on the same night. In one trial that occurred at 4 a.m., the subject and other neighbors were asleep and did not respond to either playback, so I performed the trial again three nights later when more birds were present and awake. In another case, the recorded male was present when I reached the site for the second trial, so I returned the next night and performed the trial when he was not there.

The first four trials (two pairs) included a 5-min period between the playbacks and a 5-min period after the second playback. These periods were lengthened to 10 min for the last ten trials (five pairs), in order to ensure that birds in dense neighborhoods returned to normal behavior before the second playback of each trial. The statistical analysis compared the difference in responses within subjects and thus was not affected by this change.

Measures of responses

In a separate study, I compared the features of calls by Audubon's shearwaters that were given spontaneously to the features of calls that were elicited by playbacks. In a sample of 106 calls by 14 different males, calls in response to playbacks were twice as long (8.0±0.4 s and 4.1±0.5 s, respectively), had twice the phrases (8.0±0.4 phrases and 4.3±0.5 phrases), contained more loud, wide-bandwidth notes, and had a higher peak frequency in the longest, loudest note of each phrase (Mackin 2004). In that sample, the number of phrases correlated almost exactly with the duration of the call (r^2=0.89, ANOVA, $F_{1,104}$=925.9, $P<0.0001$). Thus, the number of phrases was a simple measure of how much a playback stimulated the subject. In the dark conditions of this experiment, the simplest way to measure the responses of the subjects was to count the number of phrases.

During each trial, I counted all phrases by the subject and those by any other neighbors within 5 m of the playback. In three trials, the subject's mate was also present and her phrases were added to the total for the subject. For this paper, I analyzed only the phrases by the males. None of the results change if the data are analyzed by lumping the responses of the females and the males in these three trials. I did not analyze other responses such as the latency to respond because they were difficult to measure in the field and did not appear to vary between treatments in recordings of the experiments.

I analyzed the differences between the number of phrases in response to calls of neighbors and strangers with four separate Wilcoxon matched-pairs signed-ranks tests (subjects during and after playbacks; other neighbors during and after playbacks). The Bonferroni correction for multiple tests reduced the alpha level for significance to $0.05/4=0.0125$. I also examined the effect of the order of the playback by comparing the response to the first and second sets of calls in all 14 trials. During the trials, I was blind to the identity of the recorded callers because the recordings were identified only as randomly ordered track numbers on the mini-disc player.

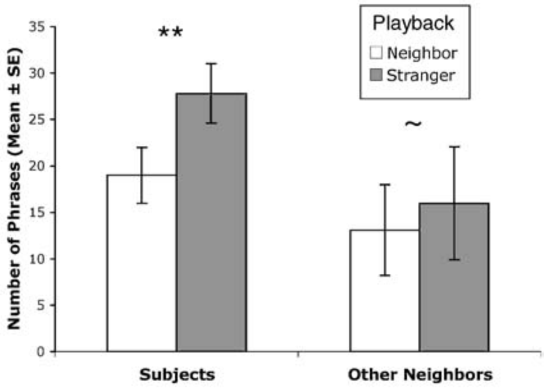
I recorded each trial in infrared light with a Sony CCD-TRV68 camera or with the audio tape system described above. In six trials, so many birds responded to the playback that it was impossible to count all phrases in the field. In those cases, I made spectrograms of the recordings with WildSpectra and counted the phrases.

Results

A subject usually responded to playbacks by moving to the entrance of its nest and calling. Only two subjects left the nest and approached the speaker during a trial. In both cases, the bird approached the calls of the neighbor and the stranger. Responding birds almost always allowed the playback to finish before they began calling, and, when multiple birds responded, each bird allowed the previous caller to finish three to five phrases before he began calling. In general, when a calling shearwater was interrupted by another bird or by a playback, it stopped calling immediately and allowed the interrupting call to finish before calling again. This pattern was conspicuous during this experiment and on other occasions when calls were played back. The chosen subject did not necessarily respond first to the playback, but he did call at least once during all of the playbacks.

Although the shearwaters responded to playbacks of both neighbors and strangers, the subjects responded with more phrases to the stranger both during (Wilcoxon Test, $T=43.5$, $P=0.002$) and after playback ($T=36.5$, $P=0.001$), while the other neighbors did not differ in numbers of phrases during ($T=7.5$, $P>0.05$) and after the playbacks ($T=-3$, $P>0.05$; Fig. 2). The order of playbacks had no significant effects on responses by the subject or the neighboring birds, either during or after the playback. ($P>0.05$ in all cases).

a) Responses during playbacks



b) Responses after playbacks

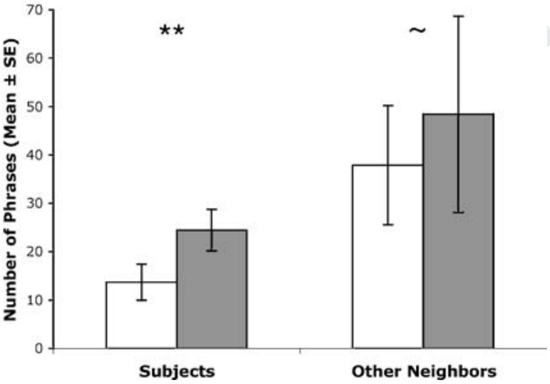


Fig. 2 Mean (±SE) number of phrases by subjects and other neighbors in response to playbacks of neighbors and strangers (**a**) during and (**b**) after the playbacks ($^{**}P<0.01$; $\cong P>0.05$)

The responses of other neighbors both during and after playbacks were in the direction of greater response to strangers than neighbors, but neither test came close to statistical significance. The other neighbors responded more to the playbacks of a neighbor during four trials, more to the playbacks of a stranger during five trials, and not at all during the playbacks in five other trials. After the playbacks, the results were similar. The other neighbors responded more after the playbacks of a neighbor in six trials, more after the playbacks of a stranger in seven trials, and not at all after one trial. To contrast those results with responses by subjects, 13 of 14 subjects responded more during the playbacks of strangers and 11 subjects responded more after playbacks of strangers. Only one subject responded more during the playbacks of neighbors, and a different subject responded more after the playbacks of neighbors.

Discussion

In response to a playback near their nest sites, Audubon's shearwaters responded with more phrases to the calls of strangers than to those of neighbors both during and after playbacks. This result is the first experimental demonstration of NSD in a bird that defends only a nest site. In order to discriminate the calls of neighbors from those of birds from other areas of the colony, the subjects must have learned the distinctive features of their neighbors' voices and classified playbacks as familiar or unfamiliar based on this memory.

The other neighboring birds provided no evidence for discrimination between neighbors and strangers. The playback speaker was closest to and directed towards the nest of the subject in each experiment, so it is likely that the other neighbors could not hear the playback as well as the subject. Because the playbacks were not immediately adjacent to their nests, the other neighbors might have responded simply to advertise their presence. Evidence from other playbacks during my study supports the latter explanation. Specifically, most birds only responded to playbacks close to their nests or when they heard one of their neighbors respond to a playback. In contrast, playbacks from 3 m or farther away from any bird's nest were usually ignored, even when they came from an active nest site. It appears that shearwaters, despite having long-term neighborhoods, do not form defensive coalitions to repel intruders (Getty 1987).

Any playbacks within a colony are complicated by the fact that several birds often call in response. The paired design of this experiment was important because it controlled for the effects of the different numbers of neighbors that were present around a subject's nest and the effects that those neighbors had on the subject's rate of calling.

Benefits of NSD for Audubon's shearwaters

Neighboring shearwaters probably represent little or no threat to each other for nest ownership. In five seasons of banding at Long Cay, I recorded ten changes of nesting males and three changes of females in 31 nests that were monitored in multiple years (about 100 nest-years). None of the ten males that took over nest sites had been observed in control of other nest sites in previous seasons. The lone observation of moving a nest was a male that nested in the open and failed to hatch its egg one year and then nested in a previously unused but more protected cavity 2 years later. Among other procellariiform birds, I have found no reports of neighboring birds competing for breeding sites. Instead, site fidelity is the norm (Mougin 1996). Replacements of males, when reported, were by birds that had not bred in the area before. While such negative evidence cannot exclude infrequent threats from neighbors, it does indicate a wide disparity between threats from neighbors and strangers.

Late in the breeding season, when I conducted my experiment, strangers were likely to have been young males prospecting for unoccupied nest sites (Bradley et al. 1999, personal observation) or for sites occupied by males that could be displaced before the start of the next breeding season. The calls of a strange male outside an established male's nest could represent a direct challenge to ownership of the site for future breeding attempts. Because established neighbors have nothing to gain by taking another bird's nest, shearwaters probably responded more aggressively to playbacks of unfamiliar voices because strangers are much more likely to take one's site than neighbors are.

The situation late in the breeding season, when these experiments were conducted, is not likely to differ from that for established breeders returning to their nests during the pre-laying period or for young males defending cavities and attracting mates. Early in the season, previous breeders should defend their nests against any males attempting to enter and neighbors are not likely to have conflicts or to have anything to compromise about. That is probably the only time of year that neighbors are any kind of threat. While NSD might break down, there will not be anything for the males to compromise about. Unpaired males seem not to compete for extensive areas in which to attract females. I have never observed such males fighting with others, but I have regularly observed them countersinging from within their nests against other unpaired males calling from their nests. Such contests were usually accompanied by females that circled overhead and alternated calling with them. Males seem to obtain nest sites first and then to compete for mates by calling from the ground to the females that fly overhead. The males in this colony also frequently countersing with females while flying above and around the island as reported for Manx shearwaters (Storey 1984; James 1985). Thus, the only benefit of NSD for shearwaters appears to be for established breeders to direct attention toward real enemies and avoid constant stimulation from the calls of other established males.

Most studies with territorial songbirds have found that NSD breaks down when the stimuli are presented from a position within a subject's territory rather than at the boundary (Stoddard 1996). The shearwaters in this study, however, responded to stimuli presented close to their nest sites rather than from the usual locations from which neighbors call. In other experiments, the shearwaters ignored playbacks that occurred from neighboring nest sites. These observations support the idea that NSD occurred because of the greater likelihood that a stranger would attempt to take the site rather than because of a conditional relationship between the subject and its neighbor.

Dear enemies, real enemies, and relative threats: Evolution and terminology

The payoffs for an Iterated Prisoner's Dilemma (Axelrod and Hamilton 1981) should often apply to species that defend all-purpose territories because each neighbor could benefit by expanding the size of its territory. Defectors interacting with neighbors that do not retaliate should have the highest payoff (a larger territory), and two cooperators should receive a higher payoff than mutual defectors. In contrast, animals that defend only nest sites might often have so little conflict with neighbors that NSD is beneficial regardless of the behavior of the neighbors.

This distinction between species that defend all-purpose territories and species that aggregate and defend only nest sites was first noted by Fisher (1954) when he used the term "dear enemy" to describe social relationships among neighbors in territorial songbirds. Temeles (1994) reviewed the known cases of NSD for all types of defended areas including two instances where subjects reacted more aggressively to familiar individuals than to strangers (Ferkin 1988; Temeles 1989, 1990). He stressed that relationships among territorial neighbors depend on the relative threats of neighbors and strangers. NSD in Audubon's shearwaters represents a special case of the relative threat hypothesis where the neighbors pose essentially no threat and the birds respond more aggressively to their real enemies, strangers.

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