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Territory defense by the ant *Azteca trigona*: maintenance of an arboreal ant mosaic

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Abstract Mosaics of exclusive foraging territories, produced by intra- and interspecific competition, are commonly reported from arboreal ant communities throughout the tropics and appear to represent a recurring feature of community organization. This paper documents an ant mosaic within mangrove forests of Panama and examines the behavioral mechanisms by which one of the common species, *Azteca trigona*, maintains its territories. Most of the mangrove canopy is occupied by mutually exclusive territories of the ants *A. trigona*, *A. velox*, *A. instabilis*, and *Crematogaster brevispinosa*. When foraging workers of *A. trigona* detect workers of these territorial species, they organize an alarm recruitment response using pheromonal and tactile displays. Nestmates are attracted over short distances by an alarm pheromone originating in the pygidial gland and over longer distances by a trail pheromone produced by the Pavan's gland. Recruits are simultaneously alerted by a tactile display. No evidence was found for chemical marking of the territory. Major workers are proportionally more abundant at territory borders than on foraging trails in the interior of the colony. The mechanisms of territory defense in *A. trigona* are remarkably similar to those of ecologically analogous ants in the Old World tropics.

Key words Ants · Territoriality · *Azteca* · Pheromones

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Introduction

Ant communities are often highly structured due to intra- and interspecific competition (Hölldobler and Wilson 1990). The "ant mosaic hypothesis" suggests that interspecific competition produces a recurring pattern of community organization among arboreal ants throughout the world's tropics (Leston 1973a, b; Majer 1972, 1976a, b; Room 1971, 1975a, b). A central claim of this hypothesis is that the numerically dominant ant species within the forest canopy defend mutually exclusive foraging territories, which nearly fill available space. Such territorial ant mosaics have been documented among canopy ants in lowland tropical forests in various regions of the world, especially in agricultural settings (Way 1953; Brown 1959; Room 1971, 1975a, b; Majer 1972, 1976a, b; Leston 1973a, 1978; Jackson 1984).

The behavioral mechanisms underlying the formation of territory mosaics are in most cases poorly understood. Although intra- and interspecific aggression have been observed frequently among tropical arboreal ants (e.g., Way 1953; Brown 1960; Vanderplank 1960; Majer 1976b), there have been few investigations of the mechanisms by which territory mosaics are produced (but see Hölldobler and Wilson 1978; Hölldobler 1979, 1983; Salzemann and Jaffe 1990). Studies from the New World tropics are particularly uncommon. Colony defense involves the coordinated actions of hundreds or thousands of workers, linked together by diverse forms of communication (Hölldobler and Lumsden 1980). This paper reports that the mechanisms of communication which allow the maintenance of mosaics are remarkably similar for two distantly related ant genera for which detailed information is available.

This study examined territory defense by the abundant Neotropical ant *Azteca trigona* (Emery) and its congener *A. velox* (Forel). Field experiments and observations were conducted within a naturally occurring ant mosaic to document the nature of the mosaic, to determine how these ants organized territory defense, to determine the role of caste in defense, and to test for the presence of a territorial pheromone (Hölldobler and Wilson 1978).

Methods

Study site and species

Studies were conducted in mangrove forests near Coco Solo, Colon Province, on the Atlantic coast of the Republic of Panama from 1983 to 1989. Vegetation characteristics are described by Adams and Levings (1987). Ants were identified by R. Snelling and vouchers have been deposited at the Los Angeles County Museum of Natural History. Because the taxonomy of *Azteca* is in need of revision (MacKay and Vinson 1989), these identifications may be subject to change.

Mapping

Maps of foraging territories were made near ground level (<2m height). In mangrove forests, ants are usually prevented from walking on the ground by tidal flooding. Nonetheless, colonies of *Azteca* spp. and other arboreal ants often forage near the water surface and rely upon connections near this level to travel from tree to tree. The lateral extent of each colony's foraging area was determined by following foraging workers and by searching the base of each tree for activity. When foraging workers were not discovered during visual scans, baits of tuna or beef were placed and monitored for 2 hr. Intraspecific boundaries were located for *Azteca* spp. (but not for a co-occurring territorial ant, *Crematogaster brevispinosa* [Mayr]) by transferring workers among baits and foraging trails to determine if fighting occurred. The edges of each territory were marked with colored flagging and mapped from central trees using a compass and tape measure.

Caste participation

To compare the caste distribution of ants defending territory borders and ants in other parts of the territory, workers were collected at different sites from 10 territories of *A. trigona*. The borders of neighboring territories are defended by dense groups of workers, whose behavior differs from that of foraging workers in the interior of the territory (Adams 1990). For each colony, workers were collected by rapidly pressing a strip of tape across a border defense group so that ants were removed before alarm responses could change the group composition. A group of workers was collected in the same manner from a major foraging trail in the interior of the colony. The head width of each ant was measured to the nearest 0.04 mm using a dissecting microscope equipped with an ocular micrometer.

To determine whether ants responding to territorial enemies were larger than ants attracted to food, baits were offered on 10 trees, each within a distinct colony of *A. trigona*. On widely separated branches, two stimuli were offered simultaneously: (1) a food bait, consisting of approximately 3 gm of tuna, and (2) a group of intruders, consisting of 3 to 5 workers of *Azteca instabilis* (F. Smith). When more than 30 workers had accumulated at a stimulus, they were collected and measured as previously described.

Glandular source of the alarm pheromone

Preliminary observations suggested that recruitment pheromones were released from the posterior end of the gaster. Three possible sources of pheromones located near the tip of the gaster – the Pavan's gland, the pygidial gland, and the hindgut – were dissected from freshly collected workers of *A. trigona* and *A. velox* and crushed in 95% ethanol. The colony from which the dissected ants had been collected was used to assay responses to the gland extracts. A fragment of the donor colony of *A. trigona* was collected and transferred to a laboratory container, measuring approximately 30 × 50 × 20 cm. The colony was provided with a paper-covered foraging arena marked with a grid of lines spaced 3 cm apart. For each test, 10 μl of fluid containing the contents of one worker's gland were used to mark a randomly selected square. After allowing 1 min for the ethanol solvent to evaporate, the ants standing within the marked square were counted. As a control, some squares were marked with ethanol alone.

For *A. velox*, a similar assay was conducted in the field. In each trial, 10 μl of extract, containing the contents of two workers' glands, were applied to a 1 cm^2 area of bark near a densely occupied foraging trail. After waiting 1 min for the ethanol to evaporate, the number of ants standing near the treated area and maintaining aggressive postures was counted. Ethanol was used as a control.

For statistical analysis, data for *A. velox* were log-transformed in order to equalize variances among responses to the four categories of extracts. This was not necessary for data from *A. trigona*. The T-method was used to evaluate unplanned comparisons among the means (Sokal and Rohlf 1981).

Glandular source of the trail pheromone

Extracts were prepared as described above. A 25 × 40 cm platform was covered with paper and placed in the field near a test colony of *A. trigona* or *A. velox*. A 1–2 m bridge connected the platform to a major foraging route of the test colony. Ants were baited to one end of the platform with beef until a group of at least 100 workers had collected around the bait. Artificial trails 25 cm in length were then drawn across the paper with a syringe, leading outward from the bait. Twenty μl of extract containing the glands from four workers were used to prepare each trail. Control trails were drawn with 20 μl of ethanol.

The ants following each trail were counted during a 3 min period. For statistical analysis, the reciprocals of counts of *A. velox* were used in order to equalize variances. Due to the lack of variation in response by *A. trigona* to two categories of trails, the Kruskal-Wallis test was used instead of ANOVA.

Territorial pheromone

Twenty colonies of *A. trigona* were chosen. Within the foraging area of each colony, a circle of filter paper 15 cm in diameter was attached to a tree trunk with dense foraging trails of *A. trigona*. The resident ants soon established trails across the paper disks. The disks were retrieved after ten days and the responses of ants to three types of paper were measured in the field: (1) paper previously occupied by their own colony, (2) paper previously occupied by a neighboring *A. trigona* colony, and (3) unoccupied controls.

To measure reactions to these three categories of paper, a wooden platform was provided in a gap between each test colony and a neighboring colony of *A. trigona*. This platform was connected to a major foraging route by a 1–2 m wooden bridge. A beef bait was placed on the platform to attract a large group of workers. Paper disks were then sequentially placed on the platform, in random order, 3 cm from the occupied bait. For each replicate, the behavior of ants approaching the paper disks and the number crossing onto the disk were recorded during a 3 min test period.

Results

The territory mosaic

Colonies of *Azteca trigona*, *A. instabilis*, and *Crematogaster brevispinosa* defended mutually exclusive forag-

Fig. 1 Foraging territories of *Azteca trigona* (horizontal lines), *A. instabilis* (solid), and *Crematogaster brevispinosa* (dots) in a mangrove forest. White areas represent unoccupied forest. Wavy lines indicate areas of open water lacking trees. Each *Azteca* polygon indicates a distinct colony. Not all intraspecific colony boundaries of *C. brevispinosa* were located; however, some were obvious due to gaps between trees. Small squares indicate isolated trees occupied by territorial ants

ing territories (Fig. 1). Although not shown in Fig. 1, colonies of *A. velox* participated in the mosaic at other locations in the mangrove forest. Ants actively defended both intraspecific and interspecific boundaries; positions were the same both day and night. Narrow unoccupied gaps (0.1 to 5 m) separated adjacent territories.

Each colony of *A. trigona* occupied several interconnected trees. On each large tree, the ants constructed one or more nests of carton, a fibrous material of paper-like consistency. *Azteca velox*, *A. instabilis*, and *C. brevispinosa* nested within existing cavities in both living and dead trees. Ants of all four species moved from tree to tree along semi-permanent trails, using branches, fallen wood, or the prop roots of the red mangrove, *Rhizophora mangle*.

Recruitment behavior

Transfers of foraging workers between colonies of *Azteca* stimulated vigorous defense: intruders were chased, immobilized and killed by groups of defending workers. The introduction of ten or more intruders stimulated alarm recruitment, sufficient to attract hundreds of nestmates. This reaction was shown intra- and interspecifically (Fig. 2).

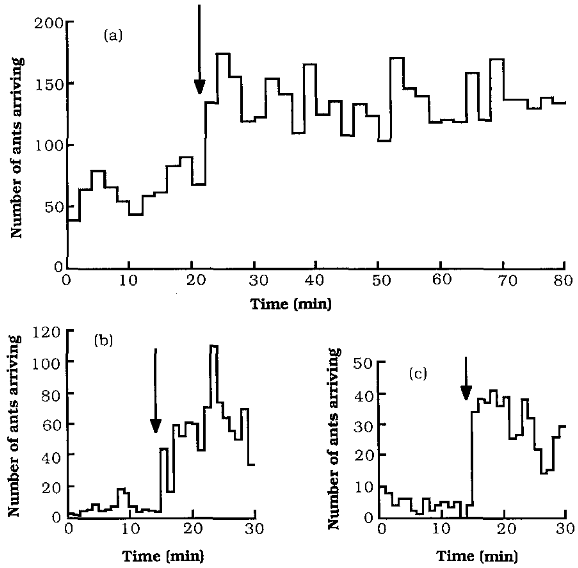

Fig. 2a–c Arrival rate of workers of *A. trigona* before and after introduction of various intruders (arrows). (**a**) 100 conspecifics from a different colony (**b**) 10 *A. instabilis* (**c**) 10 *C. brevispinosa*

Close observation revealed that three forms of communication coordinated group responses. First, ants within 5 cm of fighting nestmates began running in rapid looping motions, suggesting detection of an alarm pheromone. Alerted nestmates often adopted aggressive postures with their gasters raised and their mandibles open. Second, some ants returned to the nest in a trail-laying posture, with the tips of their abdomens pressed to the substrate. Third, a few scouts delivered a rapid tactile display to nestmates as they returned along recruitment trails. The displaying ant stood face-to-face with the recipient and shook backwards and forwards rapidly, bringing the antennae and mouthparts of the two ants into contact.

In thirty colonies, worker behavior was quantified as the ants returned to their nests following contacts with introduced opponents. On average, 20.8% ± 3.0% ($\bar{X} \pm$ SE) of returning ants deposited trails and 5.0% ± 1.4% delivered tactile displays to nestmates within 30 cm of the point of contact with their opponents ($n = 1275$ ants).

Glandular source of pheromones

For both species, alarm responses differed significantly among gland extracts and controls (Table 1). Aggressive responses to the substrates marked with contents of the pygidial glands were significantly greater than responses to other extracts or to ethanol controls (Table 1; $P < 0.05$ for both species).

In both species, workers approached and oriented along artificial trails containing the contents of the Pa-

Table 1 The number of ants responding to gland extracts or ethanol controls. Assay for alarm pheromones: $\bar{X}$ = the number of ants responding with aggressive postures to substrates marked with each fluid. Assay for trail pheromones: $\bar{X}$ = the number of workers (in 3 min) following artificial trails. Analysis of variance and the Kruskal-Wallis test were used to compare responses (see text). n = number of trials

Glandular source	Assay for alarm pheromone		Assay for trail pheromone	
	$\bar{X}\pm$SE	n	$\bar{X}\pm$SE	n
A. trigona				
Pavan's gland	5.9±0.8	15	93.8±15.8	10
Pygidial gland	9.9±0.9	15	2.3±0.8	10
Hindgut	3.0±0.6	15	0.0±0.0	10
Ethanol	2.6±0.7	15	0.0±0.0	10
	$F_{3,56}=19.7$; $P<0.001$		$H=27.3$; $P<0.001$	
A. velox				
Pavan's gland	5.7±2.0	10	17.4±4.3	10
Pygidial gland	13.3±1.6	10	4.2±1.7	10
Hindgut	1.4±0.5	10	1.0±0.5	10
Ethanol	0.7±0.2	10	0.2±0.2	10
	$F_{3,36}=22.8$; $P<0.001$		$F_{3,36}=22.6$; $P<0.001$	

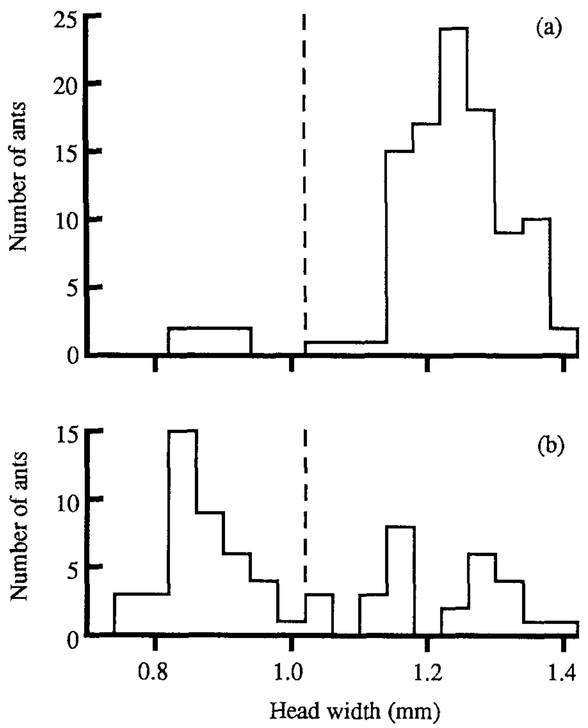

Fig. 3a, b Frequency histogram of head widths of workers collected at (**a**) a border defended against a neighboring colony and at (**b**) a foraging trail in the interior of the same colony. The dotted line indicates the division between the minor and major subcastes

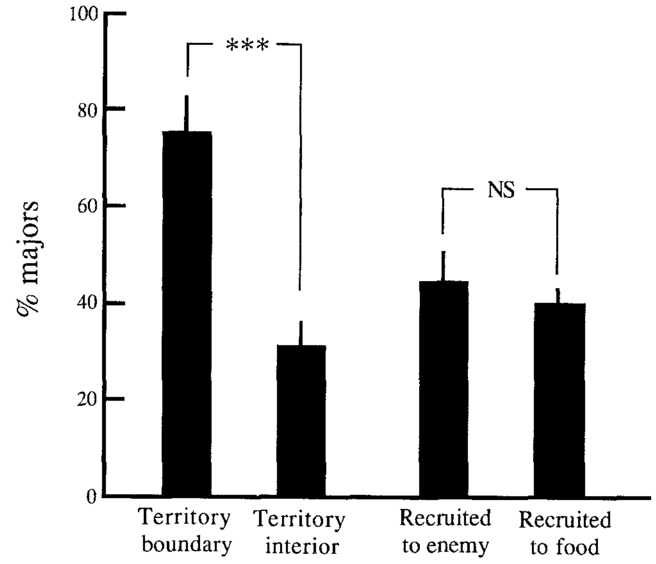

Fig. 4 The average percentage (±SE) of majors among workers of *A. trigona* collected at various regions within the territories of ten colonies. *** $P<0.001$; Mann-Whitney U test

van's gland (Table 1). A few workers responded to trails made from the pygidial gland, but these ants moved more slowly, stopping to investigate as they made their way from one end to the other. Responses to the four kinds of trails differed significantly (Table 1) with Pavan's gland extracts eliciting the strongest response.

Caste participation

The distribution of worker head widths showed a clear bimodality of size corresponding to the major and minor worker subcastes (Fig. 3; see also Wheeler 1986). The division between minors and majors was at a head width of approximately 1 mm in all ten colonies (see Fig. 3); therefore, ants with head widths greater than 1.00 mm were classified as majors. Based on this criterion, the proportion of major workers at territory boundaries was significantly higher than on foraging trails in the interior of the territory (Fig. 4; two-tailed Mann-Whitney U test, $U_{10,10}=96$, $P<0.001$). Two border defense groups were composed entirely of major workers. The proportion of major workers recruited to territorial enemies and to food did not differ significantly (Fig. 4; two-tailed Mann-Whitney U test, $U_{10,10}=61.5$, NS).

When colonies were analyzed individually, workers at territory edges were significantly larger than workers on central foraging trails in seven of ten colonies (two-tailed Mann-Whitney U test, $P<0.05$). Workers recruited to territorial enemies were significantly larger than workers recruited to food in four of ten colonies. Other comparisons of worker sizes showed no significant differences.

Test for a territorial pheromone

During 3 min tests, no differences were detected in the numbers of workers walking onto paper previously occupied by their own colony ($\bar{X} \pm$SE: 99.0±13.6), paper previously occupied by conspecific neighbors (97.4±9.3), or paper previously unoccupied by ants (78.2±15.4; $n=20$ trials for each treatment; ANOVA, $F_{2,56}=3.00$, NS). No fecal material or other marks were visible on the paper disks. No behaviors were observed in this test or in any other context that would indicate chemical marking of the territory.

Discussion

The ecological and behavioral patterns of competition in this mangrove ant community are remarkably similar to those reported for arboreal ants in other tropical regions. Colonies of four abundant species, *Azteca trigona*, *A. velox*, *A. instabilis*, and *Crematogaster brevispinosa*, defend mutually exclusive territories intra- and interspecifically. This behavior produces a mosaic of territories with well-defined boundaries. Similar mosaic patterns occur in other ant communities, especially within tropical forest canopies (Strickland 1951; Way 1953; Brown 1959, 1960; Room 1971, 1975a, b; Majer 1972, 1976a, b; Leston 1973a, b, 1978; Hölldobler 1979; Jackson 1984). Although there have been few studies of arboreal ants in Neotropical forests, *Azteca* spp. are known to defend arboreal territories in coconut plantations in Guyana (Rai 1977), in citrus crops in Trinidad (Jutsum et al. 1981), in wet forests of Costa Rica (Carroll 1979), and in secondary forest in Brazil (Leston 1978).

Territory defense is organized by pheromonal and tactile communication. Colonies of *A. trigona* and *A. velox* employ pheromones from two distinct glandular sources, allowing responses across differing spatial and temporal scales. A short-range alarm pheromone, stored in the pygidial gland, attracts nestmates over distances of several centimeters. This triggers immediate responses to intruders and pinpoints activities that shift in position. The bioactive compounds in the alarm pheromone have been identified as cyclopentyl ketones in *A. chartifex* (Wheeler et al. 1975). In addition, a long-range recruitment pheromone, originating in the Pavan's gland, is used to deposit trails, which can attract hundreds of workers across distances of several meters after a delay of several minutes. Trail recruitment to territory battles can continue for hours (Fig. 2) and may serve as the basis for semi-permanent trunk trails supplying border defense groups. These trunk trails may persist for several months or years (Adams, unpublished data). In addition to these pheromonal mechanisms, trail-laying scouts deliver tactile displays as they return from territorial battles.

The ecological significance of rapid recruitment by *A. trigona* is revealed during battles at territory boundaries. Conflicts occur when groups of workers attempt to expand their territories at the expense of neighbors. In a series of controlled field experiments, Adams (1990) showed that workers assess the relative density of nestmates and opponents during territorial battles and that workers from the outnumbered colony are more likely to withdraw. However, initial disadvantages in worker density can be overcome by rapid recruitment. Territory battles have strong effects on territory size. Maintenance of a large territory thus depends upon swift and intense recruitment, especially during the early stages of a battle.

Similar recruitment systems, with distinct long and short-range components, have been reported from other social insects in the context of foraging or defense (e.g., ants: Hölldobler and Wilson 1978; Traniello 1983; termites: Traniello 1981; honeybees: Seeley 1985 and cited references). This habit may be favored when rapid reactions are needed within large areas extending around concentrated nest populations. The long-range component attracts and directs large numbers of workers from the nests, while the short-range component orients recruits to the precise location of the stimulus.

Border defense is primarily the task of the major workers, a morphologically distinct subset of the worker caste. Majors differ from minors in head width and body allometry (Wheeler 1986). In most colonies, workers in border defense groups were significantly larger than those travelling on trails in the colony interior; indeed, some defense groups were composed entirely of majors. Among other aggressive ants with worker polymorphism, the major workers are often disproportionately involved in defense (Wilson 1976; Hölldobler 1981; Feener 1988). In some of these species, this division of labor is accomplished by caste-specific patterns of communication, with majors responding more strongly to alarm recruitment than to food recruitment (Wilson 1976; Detrain and Pasteels 1992). This does not appear to be the primary mechanism in *A. trigona*. In four of 10 colonies, recruits to territorial enemies were significantly larger than recruits to food; however, this tendency was weak and inconsistent. Recruits may be unable to distinguish these two contexts of trail communication. If this is the case, then the preponderance of major workers at colony boundaries may be caused by an increased tendency of minors to withdraw from prolonged agonistic encounters.

No evidence was found for chemical marking of the substrate. Instead, colonies of *A. trigona* actively defend boundaries by maintaining border-defense groups. The ants continually probe their neighbors, waiting for opportunities to advance into the territories of adjacent colonies (Adams 1990). By contrast, other species of ants, including *A. foreli*, mark trails or occupied substrates with colony-specific odors (Cammaerts et al. 1977; Hölldobler and Wilson 1978; Traniello 1980; Jaffe 1986), which may confer an advantage to the resident colony during territorial fights (Hölldobler and Wilson 1978).

The mechanisms of territory defense in *A. trigona* are remarkably similar to those described for ecologically analogous ants from Old World tropical forests. The best known of these are the weaver ants, *Oecophylla longinoda* and *O. smaragdina.* Like *A. trigona,* weaver ants are aggressive inhabitants of tree canopies, defend foraging space intra- and interspecifically, and possess multiple arboreal nests scattered throughout their territories (Cole and Jones 1948; Way 1954; Hölldobler and Wilson 1978; Leston 1978; Hölldobler 1979, 1983). Both genera tend homopterans, prey upon living insects, and scavenge opportunistically (Way 1954; Hölldobler and Wilson 1978). Caste structure is also similar, with a bimodal distribution of worker sizes and with division of labor between the two physical subcastes (Weber 1946, 1949; Wheeler 1986).

Furthermore, the social communication systems of *A. trigona* and *O. longinoda* are similar in many remarkable details. Workers of *O. longinoda* employ both short-range alarm pheromones and long-range trail pheromones to organize territorial responses (Hölldobler and Wilson 1978). In both species, the trail pheromone used in long-range alarm recruitment is the same as that used to recruit nestmates to large food items; however, when recruiting to territorial invaders, workers in both species deliver a tactile display to nestmates to communicate alarm (Hölldobler and Wilson 1978).

Despite these resemblances, the two ants are not closely related and the territorial behaviors appear to have evolved independently. *Oecophylla* is in the subfamily Formicinae and *Azteca* is in the subfamily Dolichoderinae. Moreover, the glandular sources of the recruitment pheromones differ between the two genera: *O. longinoda* produces trail pheromone in the rectal gland and alarm pheromone in the sternal gland (Hölldobler and Wilson 1978). Thus, it appears that any similarities in the design of territory defense and communication are due to convergent evolution.

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