

BREEDING BIOLOGY OF ROYAL AND CAYENNE TERNS AT A MIXED-SPECIES COLONY IN PATAGONIA

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ABSTRACT.—We studied the breeding biology of Royal (*Sterna maxima*) and Cayenne terns (*S. eurygnatha*) at Punta León, Patagonia, during 1989–93. In all years, both species bred in a single colony with their nests intermingled. Colony size varied between 1,150 and 1,830 pairs. Colony formation occurred during the first or second week of October. Nesting densities were relatively high (9.8 to 11.1 nests/m²). Both species started to lay eggs during the second and third week of October in all years. During 1993, clutch size for Royal and Cayenne terns was 1.3 ± 0.5 and 1.1 ± 0.3 , respectively. The length of the incubation period was 25.7 ± 0.9 and 29.1 ± 3 days for Royal and Cayenne terns, respectively. During 1993, hatching success was 0.72 ± 0.34 and 0.68 ± 0.42 chicks per nest for Royal and Cayenne terns, respectively. Egg losses (45.3%) were mainly from predation. First-hatched chicks were observed during mid November. Chick survival to 10 days of age was 90% and 66.7% for Royal and Cayenne terns, respectively. At approximately 20 days of age, some tern chicks started to abandon the colony to form creches at the beach. Royal and Cayenne terns generally fed out of sight from the colony and preyed upon the same species, including *Odontestes* spp., *Stromateus brasiliensis*, *Engraulis anchoita*, and *Sprattus fueguensis*. Received 16 Jan. 1997, accepted 3 June 1997.

Royal (*Sterna maxima*) and Cayenne (*S. eurygnatha*) terns are two widely distributed species. Royal Terns breed from eastern North America to Patagonia (Escalante 1985, Yorio and Harris, in press) while Cayenne Terns, considered by some authors as a race or color morph of the Sandwich Tern (*S. sandvicensis*) (Buckley and Buckley 1984, Gochfeld et al. 1994), breed from the southern Caribbean to Patagonia (Olsen and Larson 1995, Yorio and Harris, in press).

In Argentina, both species breed at a few locations on the Patagonian coast (Zapata 1965, Korschewski 1969, Daciuk 1972, 1976, Yorio et al. 1994). As in other regions (Bent 1921, Ansingh et al. 1960, Buckley and Buckley 1972a, Blus et al. 1979, Antas 1991), Patagonian Royal and Cayenne terns nest with each other or in association with other tern species (Zapata 1965, Daciuk 1973, Yorio and Harris, in press). On occasion, Royal and Cayenne terns breed in a single colony with their nests intermingled (Korschewski 1969, Yorio et al. 1994).

Like other species of the crested tern group, Royal and Cayenne terns have natural history traits distinguishing them from other tern species. In

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general, crested terns breed at relatively high densities, frequently change colony site location, and do not remove egg shells from the nest. They do not disperse droppings, they sit tightly on the nest when approached by predators, their chicks are precocial leaving the nest soon after hatching to form creches, and breeders readily desert the colony when disturbed (Ansingh et al. 1960, Cullen 1960, Buckley and Buckley 1972a, Langham and Hulsman 1986). These traits appear to be anti-predator adaptations (Cullen 1960).

Royal and Cayenne tern breeding biology has been described at only a few locations in the United States (Kale et al. 1965, Buckley and Buckley 1972a, Blus et al. 1979) and the Caribbean (Ansingh et al. 1960). Other studies have described some aspects of their taxonomy (Junge and Voous 1955, Voous 1968, Buckley and Buckley 1984, Escalante 1984), distribution (Voous 1963, Ffrench and Collins 1965, Sick and Leao 1965, Zapata 1965, Buckley and Buckley 1984, Escalante 1991), feeding ecology (Buckley and Buckley 1974, Erwin 1977, 1978), and behavior (Ashmole and Tovar 1968, Buckley and Buckley 1970, 1972b, 1977, Grant 1981, Kilham 1981). Conservation problems of these species have been discussed by Daciuk (1973), Escalante (1982, 1985), Antas (1991) and Gochfeld et al. (1994). In the present paper, we describe the breeding biology of Royal and Cayenne terns at the Punta León mixed-species colony and compare our results with those of studies at other locations.

METHODS

Punta León (43°04'S, 64°29'W) is 10 km south of the mouth of Golfo Nuevo, Patagonia. The coast in this area is characterized by extensive cliffs 30–100 m high and gravel beaches along the shoreline. About 700 m of shoreline are separated from the cliffs by a silt platform of approximately 5 ha, covered by vegetation consisting mainly of *Suaeda divaricata*, *Atriplex lampa*, and *Lycium chilense*, and is used as nesting substrate by several seabird species. Seabirds breeding with Royal and Cayenne terns include Kelp Gulls (*Larus dominicanus*), Imperial Cormorants (*Phalacrocorax atriceps*, with both "atriceps" and "albiventer" color morphs), Olivaceous Cormorants (*P. olivaceus*), Rock Shags (*P. magellanicus*), and Guanay Cormorants (*P. bougainvillii*) (Malacalza 1987, Yorio et al. 1994).

To analyze the variation in numbers of both tern species within each season, we made weekly censuses throughout the 1989–1992 breeding seasons. We made counts with spotting scopes 20–45× from an observation point located on cliffs at a distance of 50–70 m from the colony. Early in the season when colony size was small, we obtained numbers by direct count of birds. Later in the season, we estimated the number of birds within a small area and extrapolated that count to the total colony area. We calculated the proportion of breeding pairs of each tern species by counting their nests along 10–30 imaginary transects covering the whole colony.

We estimated population size of both tern species from aerial photographs taken during peak egg laying (21 Nov. 1989, 7 Nov. 1990, and 15 Nov. 1993). We used a Cessna 182, flying at an altitude of 100–300 m, and took photographs with 80–200 and 300 mm lenses. We obtained total numbers of breeding pairs through counts by the two of us from projected

slides. We considered as "breeding pairs" all birds sitting as if they were incubating, birds standing on a scrape, and pairs of birds standing either within or at the periphery of the colony.

We calculated nesting densities after the breeding season was over by randomly sampling 1 m² quadrats within the colony. All nests with more than half of the nest cup within the quadrat were included in the count. We analyzed the distribution of nests using the Clark and Evans test (Rabinovich 1980). During all seasons, we obtained information on habitat characteristics from the observation points on the cliff.

Both terns are highly sensitive to human disturbance (Buckley and Buckley 1972a, Daciuk 1972, 1973, Escalante 1985, Antas 1991). Therefore, we obtained information through observations from the cliffs (1989–1993), from a blind (1993), and through automatic video recordings (1992–1993). During each season, we gathered data on colony formation, egg-laying and chick hatching dates, colony abandonment by adult birds and chicks, and creche formation on the beach from cliff observations.

During 1992 and 1993, we monitored 27 and 58 nests, respectively, of both tern species using an automatic video camera located at the periphery of the colony. Recordings were made at regular intervals through daylight hours from settlement to hatching. During 1993, we also identified and monitored 36 Royal Tern and 28 Cayenne Tern nests from a mobile blind located 1–2 m from the tern colony. We previously tested the effects of the mobile blind by making gradual approaches to the nesting birds, never observing nest abandonment. Using maps, we identified all study nests every two days and recorded adult presence, stage of the breeding cycle, and number of eggs or chicks. We categorized nests by species (Royal or Cayenne) and location within the colony (central or peripheral). We defined as peripheral any nest that was not completely surrounded by other tern nests. These were generally located in the first or second row from the edge of the colony.

We estimated egg losses from predation by assuming that disappeared eggs had been preyed upon. We estimated chick survival to the first ten days of age, as approximately at that age chicks start to move within the colony and individuals cannot be followed if unmarked. We did not mark chicks to avoid disturbance and, therefore, we could not obtain information on chick survival after 10 days.

During 1992 and 1993, we obtained information on the prey captured by both tern species during the chick stage through observation of adults arriving with food at the colony. Like other terns, both species at Punta León bring food back to the colony carrying only one prey item in the beak per trip. We identified prey species through direct observation from the blind and cliff using binoculars and spotting scopes.

RESULTS

Royal and Cayenne terns started to arrive at Punta León in mid-September and remained courting and mating on the beach for up to a month before finally settling in the colony site. Between arrival at Punta León and final settlement in the colony, terns stayed in the area for only a few hours a day, but during the evenings there was an increase in the number of individuals.

At Punta León, courtship and copulation behaviors occurred mainly on the beach and were similar for both species. Behaviors observed consisted of terrestrial and aerial displays, both including courtship feeding. Courtship behavior of both tern species was similar to that described elsewhere

for these species (Buckley and Buckley 1972a, Kilham 1981) and for other crested terns (Cullen 1960, Smith 1975).

During all seasons, settlement at the colony site occurred during the second or third week of October. Colony formation was always initiated by a group of about 100–150 Royal Terns and the colony grew through the gradual settlement of new groups of both species at the periphery. As a result, both species bred in a single colony with their nests intermingled. During all years, Cayenne Terns started nesting after the first group of Royal Terns started laying eggs. Nesting rate for both species was lower in 1991 than in previous years (Fig. 1). The number of terns at the colony increased rapidly during the second and third week of October and reached a maximum during the first or second week of November, depending on the breeding season (Fig. 1). Colony size varied among seasons (Table 1).

In all seasons, the colony was located 10–20 m from the high tide line and approximately 1 m above sea level. Nests were located in sections of bare ground surrounded by *S. divaricata* bushes up to 1.5 m tall. In all years, the colony was located within the Kelp Gull colony, and therefore was always surrounded by gull nests. Kelp Gulls start nesting more than a month before Royal and Cayenne terns (Yorio et al. 1994) and nests both on bare ground and under vegetation (Yorio et al., in press). The location of the colony was variable between years. Royal and Cayenne terns settled during the first three years close to the north end of the cormorant colony, but during 1991 they moved approximately 150 m to the south to another section of the Kelp Gull colony, where they nested up to 1994.

Tern nests consisted only of a scrape on the bare ground, made with their feet while sitting. Nests were evenly distributed throughout the open space and packed close together, showing hexagonal packing similar to that described by Buckley and Buckley (1977). Nests had a homogeneous distribution (Clark and Evans test, $r = 33.2$). Nesting densities were relatively high (Table 2), and the average distance between adjacent nests was 29.8 ± 2.6 cm ($N = 29$) for 1989 and 31.4 ± 2.4 cm ($N = 40$) for 1992.

First eggs were laid between the second and third week of October in all years. Most pairs laid their eggs on the same day that they settled in the colony site. No significant differences were found between the clutch sizes of Royal and Cayenne terns (Mann-Whitney Test, 1992: $U = 32.5$, $P > 0.1$; 1993: $U = 178.5$, $P > 0.1$; Table 3).

During all years, pairs reused nest sites that had been used and abandoned by individuals of the same or the other species. For example, 28% of Royal Tern nests studied during 1993 ($N = 36$) were reused by Cay-

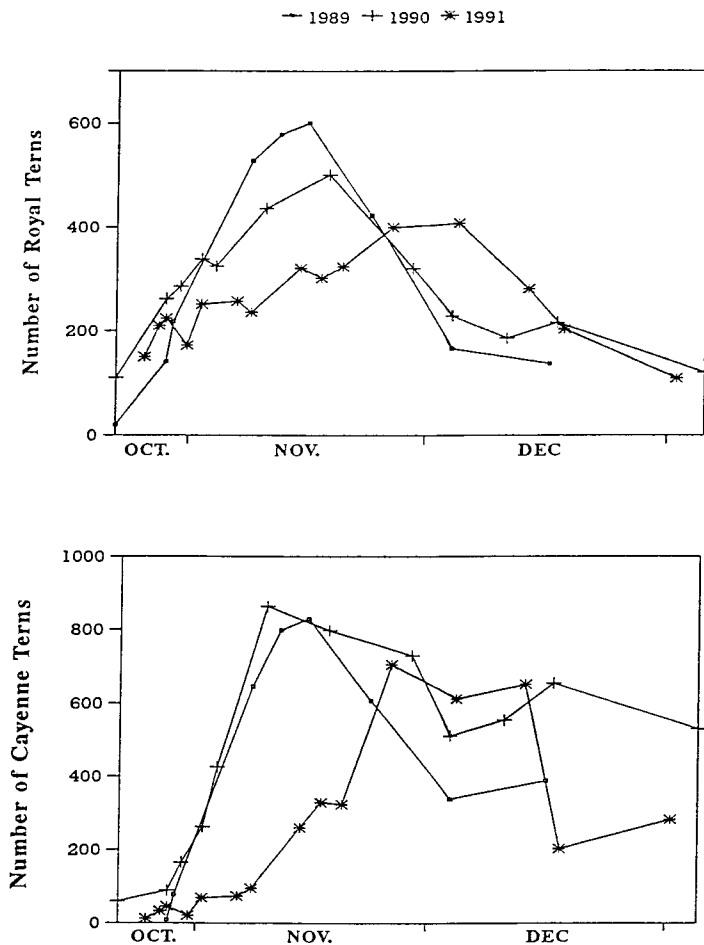


FIG. 1. Number of Royal and Cayenne terns as a function of time within the 1989–91 reproductive seasons.

enne Terns and 11% of Cayenne Tern nests ($N = 28$) were reused by Royal Terns.

The length of the incubation period (monitored daily from egg laying to egg hatching using the video camera) was 25.7 ± 0.9 days ($N = 6$) for Royal Terns and 29.1 ± 3.0 days ($N = 25$) for Cayenne Terns. Similarly, the length of the incubation period for 16 Royal Tern nests that were monitored from the blind was between 25 and 28 days. In all cases, the incubation period was similar to that observed for the same species

TABLE 1
NUMBER OF BREEDING PAIRS OF ROYAL AND CAYENNE TERNS AT PUNTA LEÓN DURING THE 1989, 1990, AND 1993 BREEDING SEASONS

Year	Number of breeding pairs		Total
	Royal Tern	Cayenne Tern	
1989	497	656	1153
1990	687	1140	1827
1993	—	—	1565

at other locations (Ansingh et al. 1960, Buckley and Buckley 1972a, Blus et al. 1979).

Hatching success was similar for both tern species (Mann-Whitney Test, 1992: $U = 46.5$, $P > 0.1$; 1993: $U = 218.5$, $P > 0.1$; Table 3). Of 64 Royal and Cayenne tern nests studied from the blind during 1993, 45.3% were preyed upon. All nests that lost eggs from predation were peripheral. Eggs disappeared from 78.4% ($N = 37$) of the peripheral nests. Kelp Gulls are the main predator of tern eggs at Punta León (Yorio and Quintana, in press). Nest desertion was low, as only one pair of each species deserted their nest during the incubation period. Heavy rains were also a cause of egg losses at the Punta León colony during 1993 when at least 30 pairs of both tern species, not included in the study sample, lost their eggs because of nest flooding. However, heavy rains are infrequent in the study area.

First-hatched chicks were observed during the first and second week of November, except in 1991, when they started hatching during the third week of November. During the first few days after hatching, chicks of both species remained at the nest, mostly under their parents. At three or four days of age, chicks started to move up to 0.5 m away from their nest. Of 20 Royal Tern chicks hatched in 1993, 90% survived up to 10

TABLE 2
NESTING DENSITIES FOR ROYAL AND CAYENNE TERNS AT PUNTA LEÓN DURING THE 1989 TO 1992 BREEDING SEASONS (N = NUMBER OF QUADRATS)

Year	Nesting density (nests/m ²)
1989	11.1 $\pm$ 1.25 ($N = 20$)
1990	11.1 $\pm$ 1.39 ($N = 26$)
1991	9.8 $\pm$ 1.21 ($N = 29$)
1992	10.0 $\pm$ 1.50 ($N = 29$)

TABLE 3
CLUTCH SIZE AND HATCHING SUCCESS OF ROYAL AND CAYENNE TERNS DURING 1992 AND 1993 AT PUNTA LEÓN

	Percentage of nests		Clutch size (Mean $\pm$ SD)	Hatching success (Mean $\pm$ SD)	Number of monitored nests
	1 egg	2 eggs			
1992					
Royal Tern	59	41	1.4 $\pm$ 0.5	0.79 $\pm$ 0.24	22
Cayenne Tern	100	0	1.0 $\pm$ 0.0	0.60 $\pm$ 0.49	5
1993					
Royal Tern	67	33	1.3 $\pm$ 0.5	0.72 $\pm$ 0.34	9
Cayenne Tern	86	14	1.1 $\pm$ 0.3	0.68 $\pm$ 0.42	49

days of age, while of six Cayenne Tern chicks, 66.7% survived to that age.

At least one parent remained attending the nest until chicks were approximately 20 days of age. At that age, some tern chicks abandoned the colony to form creches at the beach. Other chicks remained alone or in groups within the colony or started to form groups at the colony periphery. These chicks remained at the colony for more than a month before moving to the beach. The first mixed-species creches were always observed in early December, and chick groups at the beach were highly mobile.

Royal and Cayenne terns generally fed out of sight at the observation point at the cliff. When observed foraging within 500 m from the colony, they did it alone or in groups of 5–20 individuals. Royal and Cayenne terns preyed upon the same food species (Fig. 2). These included silversides (*Odontestes* spp., Fam. Atherinidae), juvenile butterfish (*Stromateus brasiliensis*; Fam. Stromateidae), Argentine anchovy (*Engraulis anchoita*; Fam. Engraulidae), and Fueguian sprat (*Sprattus fueguensis*; Fam. Clupeidae). On only one occasion did we see a Royal tern carrying Argentine red shrimp (*Pleoticus muelleri*; Fam. Solenoceridae).

DISCUSSION

In all seasons, nesting started with a group of Royal Terns, around which the colony expanded gradually and continuously through the establishment of groups of both species at some sectors of the colony periphery. Site occupation by dense groups of birds has been previously reported for Sandwich Terns (Taverner 1970, Veen 1977) and Elegant Terns (Barrie 1975, Villa Ramirez 1976), and it is argued that it could be an important factor determining the outcome of interspecific competition

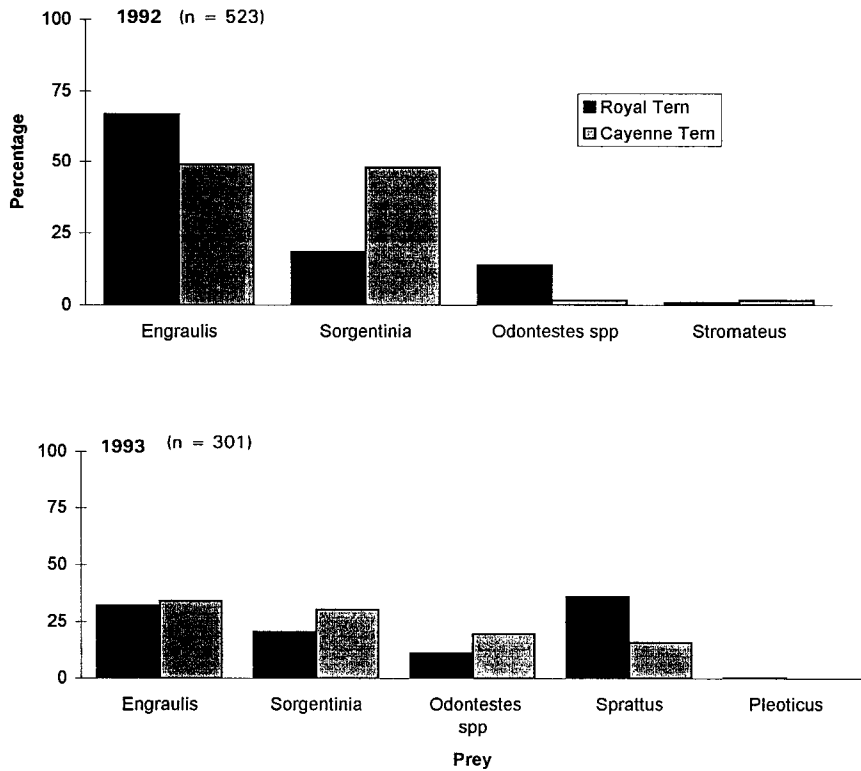


FIG. 2. Percentage of occurrence of prey types brought to the Punta León colony by Royal and Cayenne terns during the early chick stage in 1992 and 1993.

for nest sites (Burger 1985). At Punta León, this nesting behavior allows both tern species to displace already nesting Kelp Gulls and, therefore, compete successfully for nest sites with this larger and earlier-nesting species (Quintana 1995). Royal and Cayenne terns bred every year within the Kelp Gull colony. Terns might be gaining a protective advantage by moving into the gull colony if the access of potential predators were prevented by gull territorial behavior (Yorio and Quintana, in press).

In all years, Royal and Cayenne terns nested at relatively high densities, a common trait of the crested tern group (Cullen 1960, Ansingh et al. 1960, Buckley and Buckley 1972a, Langham and Hulsman 1986). At Punta León, nest densities were higher than those found in other crested terns (Langham 1974, Langham and Hulsman 1986), and previously reported in Royal Terns (7.4 nests/m², Buckley and Buckley 1972a), but lower than those observed at colonies where Cayenne Terns nest in mono-

specific clusters (12–13 nests/m², Ansingh et al. 1960). Royal Terns are larger than Cayenne Terns (Olsen and Larsson 1995) which could explain the intermediate nest densities found in the mixed-species colony at Punta León when compared to monospecific clusters of each species at other locations.

Nesting at high densities has been frequently cited as one of the main adaptive advantages of coloniality, as it reduces predation (Wittenberger and Hunt 1985). Buckley and Buckley (1972a, 1977) concluded that high nesting densities in Royal Terns have evolved as a result of low availability of nesting space and extreme egg predation by gulls on the periphery of the colony. At Punta León, egg predation by Kelp Gulls is the main factor affecting tern breeding success (Yorio and Quintana, in press), and predation occurred mainly on peripheral nests. High-nesting densities of Royal and Cayenne terns at Punta León appear to be an important factor in decreasing predation on central nests by aerial predators (Yorio and Quintana, in press). Similar findings have been reported for other crested terns, where peripheral nests were more susceptible to predation by gulls than central nests (Buckley and Buckley 1972a, Langham and Hulsman 1986).

Early formation of chick groups and colony abandonment, a trait found in the crested tern group, was also observed at Punta León. However, chicks started grouping and leaving the colony after they were more than three weeks of age, significantly later than was observed for Royal and Cayenne terns in previous studies (Ansingh et al. 1960, Buckley and Buckley 1972a). Those studies indicated that the formation of chick groups within the colony and colony abandonment occur a few days after hatching, similar to the Sandwich Tern (Cullen 1960, Smith 1975) and Crested Tern (*Sterna bergii*) (Langham and Hulsman 1986). The differences found in the timing of colony abandonment and creching by chicks could be due to a different degree of disturbance between the studies. Smith (1975), for example, found that colony abandonment was earlier in colonies of Sandwich Terns subject to human disturbance. Several studies on crested terns describe the high mobility chicks show in response to investigator approaches, while the study at Punta León was conducted without entering the colony, thus minimizing the disturbance.

Both tern species at Punta León fed mainly out of sight of the coast and captured the same prey species. For both terns, diet was similar in both study seasons, except for the presence of the Fueguian sprat in 1993. Fueguian sprat are not regularly found in the study area and are only occasionally recorded as a result of the intrusion of cold water currents from the south (G. Caille, Universidad Nacional de la Patagonia, pers. comm.).

One of the main features of the Punta León colony is the close association between species during nesting. Royal and Cayenne terns breed in a single group with their nests intermingled and at relatively high densities. This type of mixed-species colony has not been described for other tern species and has only been reported by Korschenewski (1969) for Royal and Cayenne terns breeding at Punta Tombo, Chubut, Argentina. Both species have been previously described as breeding in discrete groups within less dense colonies of other species such as South American Terns (*S. hirundinacea*) and Common Terns (*S. hirundo*) (Bent 1921, Ansingh et al. 1960, Buckley and Buckley 1972a, Daciuk 1973, Blus et al. 1979, Antas 1991).

The nesting association between Royal and Cayenne terns also occurs at other coastal locations in Patagonia, such as southern Buenos Aires, southern Chubut, and northern Santa Cruz (Pérez et al. 1995, Yorio and Harris, in press). This nesting association appears to be possible because of the similar breeding strategies of both tern species. Our results show that both terns have a wide overlap in habitat requirements and timing of breeding and, apparently, feed on the same prey species. The reasons why both species associate in this way during breeding are not clear, although it might be advantageous for Royal and Cayenne terns to nest together to reduce predation. Given the high density of the mixed-species tern colony, it is difficult for avian predators to steal eggs from central nests, leaving only peripheral nests vulnerable to predation. Therefore, an increase in the size of the colony as a result of the mixed nesting of both species would be advantageous as it reduces the number of exposed nests in relation to total colony size.

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