ANTIPREDATOR BEHAVIOUR IN NESTING ZENAIDA DOVES (ZENAIDA AURITA): PARENTAL INVESTMENT OR OFFSPRING VULNERABILITY

by

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Introduction

For most organisms successful survival and reproduction depends on predator avoidance. Nesting birds avoid predation by relying on cryptic coloration, nesting in inaccessible locations (LACK, 1968), possessing antipredator behaviours to defend themselves or their chicks (TINBERGEN, 1953; KRUUK, 1964), relying on the antipredator behaviour of other individuals or species (NUECHTERLEIN, 1981; BURGER, 1984), or a combination of the above. The nest dispersion pattern of birds is often a compromise between nesting far apart for crypsis, and nesting in dense groups that can contribute predator defense and increased vigilance for the colony (TINBERGEN et al., 1967). Species that normally nest solitarily, such as shorebirds, often nest in colonies of other species to gain the advantage of their vigilance and antipredator behaviour (KOSKIMIES, 1957; ERICKSSON & GOTMARK, 1982). Such species may also exhibit antipredator behaviours, such as distraction displays to decoy predators away from the nest (NICE, 1923; GOCHFELD, 1984).

Antipredator behaviour involves risk to the parent, as well as increased time and energy costs. Presumably offspring survival can be enhanced by the antipredator behaviour of the parents, and such care must be a compromise between the benefit to the present brood, and survival of the parent for future broods (TRIVERS, 1972). Two hypotheses have been proposed to account for defense behaviour. TRIVERS' (1972) cumulative parental investment hypothesis predicts that nest defense should increase

throughout the breeding cycle because the cost of the offspring (or the total parental investment) is increasing. Alternatively, SKUTCH (1949) and ANDERSSON *et al.* (1980) have proposed that the level of nest defense should correspond to the vulnerability of the offspring.

In this study we test these alternative hypotheses by examining the antipredator behaviour of zenaida doves (*Zenaida aurita*) nesting on seven islands in the Culebra archipelago, Puerto Rico. We determined how antipredator behaviour varies as a function of stage in the reproductive cycle, whether the behaviour of doves nesting within seabird colonies differed from those nesting outside colonies, and whether their nest departure and antipredator behaviour differed as a function of habitat. Changes in antipredator behaviour indicating changing parental investment occur during the nesting cycle in colonial species that mob predators (ERWIN, 1979), and may also occur in solitary-nesting species. Moreover, differences in the behaviour of otherwise solitary nesting species that nest within and outside colonies of other species have not been examined.

On the islands around Culebra, zenaida doves nest in a variety of habitats from cliffs and rocky outcroppings to under dense herbaceous vegetation and low shrubs (BURGER *et al.*, 1989). They nested in all available habitat types on the two islands studied, although they nested closer to terns (*Sterna* spp.) than expected. On mainland Puerto Rico zenaida doves nest in forest edge, mangrove forests, dry scrub and mixed agriculture and urban areas (J. W. WILEY, pers. comm). They nest primarily in trees in Puerto Rico, contrary to their nest site choices on Culebra. NELLIS *et al.* (1984) reported that on St. Croix, St. Thomas, and the U.S. Virgin Islands zenaida doves nested in grass, bushes, ledges, ground, trees, and rocks, but they did not provide relative use estimates. Most studies characterize the nesting habitat as bushes and trees (GOSSE, 1847; BIAGGI, 1970; RAFFAELE, 1983). Elsewhere (BURGER *et al.*, 1989) we describe their preference for nesting in seabird colonies, a feature not remarked on by other authors.

Study area and methods

We surveyed ten islands or cayos for nesting zenaida doves: Raton, Agua, Geniqui, West Lobito, Matojo, Molinos, Yerba, Lobo, Botella and Sombrerito. The latter three islands contained no breeding doves and no breeding seabirds. Thus we will discuss only the former seven.

Raton (1.8 ha) is dome shaped with 20 m high cliffs and steep vegetated slopes (mostly *Conocarpus erectus, Cyperus planifolius*). Agua (3.7 ha) has low cliffs with a flat top with low, dense, mixed-species vegetation. Geniqui (West, 4.4 ha) has sheer cliffs on all sides with a dense stand of *Cyperus planifolius*. Lobito (6.1 ha) has low cliffs and is dome-shaped,

covered with dense, low vegetation, predominantly *Capparis flexuosa*. Matojo (0.8 ha) also has low cliffs and a plateau covered with small shrubs and vines and is dominated by *Canavalia maritima*. Molinos (1.1 ha) is a small, tilted, rocky island with barren, jagged rocks, and a stand of sea grape (*Coccoloba uvifera*) and buttonwood (*C. erectus*). Yerba (1.9 ha), a tilted plain, is surrounded by steep cliffs and is mainly covered with *Cyperus planifolius*. Table 1 lists the avian species composition on each island; further descriptions can be found in KEPLER & KEPLER (1978), FURNISS (1983), DELANNOY (1983), and BURGER & GOCHFELD, 1985, 1986, 1988).

Based on previous work, we timed our visit (late May) to correspond to the middle of the breeding season, so that we could observe doves in different breeding stages. We visited all islands once, surveying the entire island for dove nests. Survey methods consisted of walking slowly along transects over the entire island, watching for the emergence of doves. When a dove was spotted we noted the behavior of the departing dove, marked our location, and walked to the place where the dove first appeared, to search for the nest. For each dove nest located we recorded: island, date, time of day, stage, number of eggs or young, age of young (0 to 14 days), species and distance to closest neighbor, whether the nest was within a seabird colony, distance to the colony edge, species of the colony, flush distance, method of leaving the nest, behaviour following nest departure, time the bird remained near the nest, how far the dove flew or walked from the nest, and number and species of birds overhead. All behaviours following nest departure, particularly distraction displays, were described in terms of distance from the observers, length of display, and form of the display.

TABLE 1. Species composition of islands studied in Culebra archipelago.
Shown are approximate number of nests

	Aqua	Geniqui	Raton	Lobito	Matojo	Molinos	Yerba
Zenaida dove							
Zenaida aurita	51	35	24	15	4	2	14
Red-billed tropicbird							
Phaeton aetherus			2				
Brown boody							
Sula leucogaster		39					
Audubon's shearwater							
Puffinus Pherminieri	6			3			
Laughing gull							
Larus atricilla		140		350	160		
Roseate tern							
Sterna dougallii			30			48	
Bridled tern							
Sterna anaethetus	45	15	38	48	21	20	18
Sooty tern							
Sterna fuscata						275	12,000
Sandwich tern							
Sterna sandvicensis					4		
Royal tern							
Sterna maxima					30		
Brown noddy							
Anous stolidus		52				88	

These procedures required two people for the approach, and each person moved slowly so that we could pinpoint the exact place where the dove flushed. We had experience in the previous year searching for dove nests and learning to note our position and that of the flushed bird.

We used multiple regression procedures to determine the factors that affected flush distance, time that the bird remained near the nest, and distance the dove flew from the nest. The independent factors used for the statistical models included: distance to colony edge, stage, island, stage × island, nearest neighbour distance, and age of chick. This procedure enters the variable that contributes the most to the variation, and then enters the second variable that adds the most to the r^2, thus minimizing the impact of correlation among variables. We then used Kruskal-Wallis χ^2 to determine significant differences among the distributions of the variables.

Results

Departure behaviour.

Zenaida doves depart from their nests by surreptitiously walking away, by flying, or by bursting explosively in flight from the nest when an intruder is very close. Overall, most doves initially flew from the nest (Fig. 1). Departure behaviour was followed by continued walking, continued flying (sometimes out of sight), flying in circles around the nest, or giving distraction displays. Doves that walked away usually continued to walk and then flew away, flew and then gave a distraction display, or gave a distraction display (Fig. 1). Doves that initially flew away either watched us, circled, or gave a distraction display, and those that burst explosively from the nest always gave distraction displays.
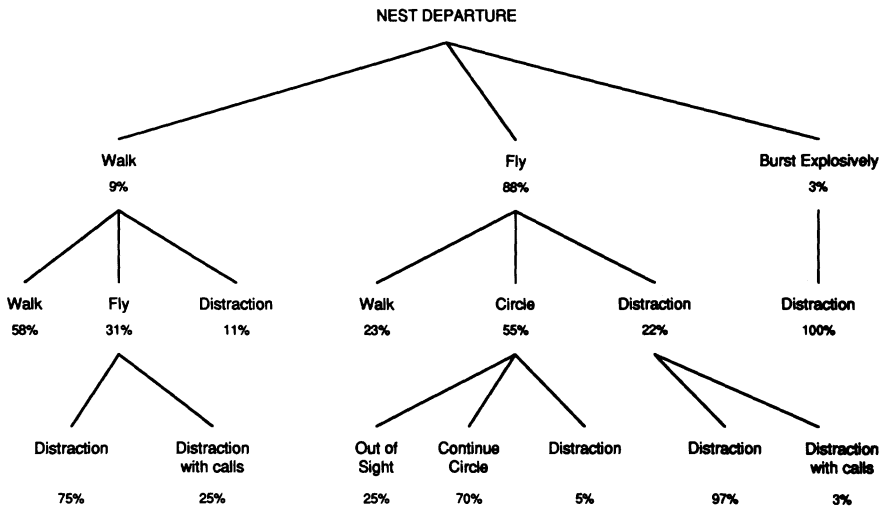

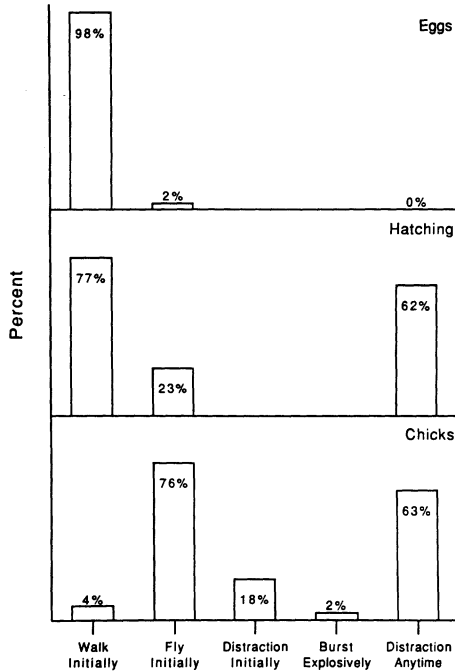Fig. 1. Sequences of behaviour for zenaida doves when disturbed (n = 145).

Fig. 2. Initial departure behaviour of zenaida doves as a function of reproductive stage.

Initial departure behaviour varied by reproductive stage (Fig. 2). Parents with eggs usually walked from the nest, parents with hatching eggs usually walked or flew from the nest, and parents with chicks flew initially or gave distraction displays.

Distraction displays.

In all cases only one parent was present at the nest. Some zenaida doves gave distraction displays following nest departure. Birds giving distraction displays flew and landed 1 to 30 m from us ($\bar{x} = 8.5$ m, SE = 7.5, N = 37). In three cases, doves with 1-2 day old chicks did not flush until touched, and then they flopped to the ground and began giving a distraction display. Distraction displays usually involved fluttering against the ground or rocks with both wings extended and the tail spread. In about a third of the cases the birds flopped to one side as if one wing was injured. Doves fluttered slowly away from us for 1 to 3 minutes ($\bar{x} = 2.1$, SD = 1.7 min). We only remained for 5-6 min at each nest, and the doves usually circled aerially about us for the remaining time we were near the

nest. Fewer distraction displays occurred following walking nest depar-
tures compared to flight nest departures (Fig. 1). Clearly birds that
walked surreptitiously from the nest were less likely to give distraction
displays, and did not remain in the area circling about us.

Factors affecting nest departure and distraction behaviour.

Birds departing from the nest flushed when we were at a particular
distance from the nest, flew a certain distance, and remained near the
nest for variable periods of time. Variability in flushing distance was
explained by breeding stage and island; variability in distance flown from
the nest was explained by stage, island, and distance to colony edge; and
variability in time to remain near the nest was explained by stage, island,
distance to colony edge, and stage × island (Table 2).

TABLE 2. Models explaining variation in nest departure

	Flush distance	Distance flown from nest	Time to remain near nest
Model			
r^2	.29	.94	.43
F	1.94	53.80	4.01
P	.02	.0001	.0001
Factors entering			
Distance to colony edge		130.6 (.0001)	7.17 (.009)
Stage	2.64 (.05)	4.89 (.01)	9.37 (.001)
Island	4.85 (.0006)	132.11 (.0001)	2.09 (.06)
Stage × island			2.77 (.009)

For factors entering, given are F value and level of significance.

Nearest neighbour distance was greatest on Agua, Yerba and Lobito (of the
islands with more than 14 pairs of doves) and lowest on Geniqui and
Raton (Table 3). As expected, there were no significant differences in
nearest neighbour distance as a function of breeding stage either for the
combined data, or for Agua alone. Only the three islands with over 20
dove nests are shown in Table 4. Most doves had conspecifics for nearest
neighbours (Fig. 3).

Flush distance was greatest on Yerba, Agua and Lobito, and lowest on
Geniqui and Raton (Table 3). Thus, nearest neighbour and flush
distances seemed related. Flush distance also varied significantly by
breeding stage, with incubating parents flushing at greater distances than

TABLE 3. Behaviour of doves at 131 nests as a function of island and stage in breeding cycle

	N	Nearest neighbor distance (cm)	Flush distance (cm)	Time remaining around nest (sec)	Distance flown from nest (m)
Island[a]					
Aqua	51	446 ± 27	389 ± 43	21 ± 6	27 ± 5
Geniqui	35	249 ± 20	200 ± 25	5 ± 5	21 ± 2
Raton	24	321 ± 40	185 ± 20	66 ± 30	47 ± 22
Yerba	14	460 ± 43	444 ± 250	—[b]	—[b]
Lobito	15	400 ± 39	321 ± 52	38 ± 17	16 ± 4
Matojo	4	552 ± 119	225 ± 131	7 ± 7	12 ± 1
Molinos	2	220 ± 100	335 ± 215	—[b]	200 ± 10
χ^2		32.8	13.3	12.9	13.7
df		6	6	4	5
P		.0005	.02	.01	.02
Stage					
No eggs	5	450 ± 50	481 ± 193		
Eggs	76	338 ± 20	317 ± 26	11 ± 6	38 ± 9
Eggs and chicks	12	485 ± 67	193 ± 46	37 ± 12	21 ± 4
Chicks	38	376 ± 29	237 ± 45	63 ± 20	28 ± 10
χ^2		5.91	8.17	28.81	17.8
df		3	3	2	2
P		NS	.05	.0001	.0001

Given are means ± one standard error. [a] Using only the first islands, χ^2 values were all significant at P values of < .0001, 005, .01 and .05. [b] Because of topography, it was difficult to determine how far they flew.

parents with chicks (Table 3). This difference also occurred on Agua and Geniqui (not tested because of small sample sizes), but not on Raton (Table 4).

Time remaining near nest was greatest on Raton, and least on Yerba and Geniqui. Geniqui also had the highest percent of nests with eggs. Breeding stage significantly affected the time parents remained near the nest. For the combined data and for the islands separately parents with chicks remained near the nest for longer than those with eggs (Tables 3, 4).

Distance flown from the nest. Other than Molinos, doves on most islands flew between 12 m and 47 m away (Table 3). Parents incubating eggs flew further away than those with chicks for the combined data and for the three islands with the highest sample size (Tables 3, 4).

TABLE 4. Behaviour of doves on several islands as a function of breeding stage

	N	Nearest neighbor distance (cm)	Flush distance (cm)	Time remaining around nest (sec)	Distance flown from nest (m)
Agua					
eggs	26	426 ± 41	438 ± 49	14 ± 6	43 ± 10
eggs and chicks	6	545 ± 66	209 ± 100	40 ± 18	20 ± 2
chicks	17	436 ± 47	319 ± 97	35 ± 14	17 ± 4
χ^2		2.03	6.55	6.32	5.82
df		2	2	2	2
P		NS	.03	.04	.05
Geniqui West[a)]					
eggs	31	245 ± 21	214 ± 28	6 ± 5	27 ± 2
eggs and chicks	3	410 ± 2	150 ± 12	38 ± 6	17 ± 2
chicks	2	190 ± 30	67 ± 17	40 ± 0	5 ± 2
Raton					
eggs	8	363 ± 53	178 ± 41	42 ± 2	88 ± 26
eggs and chicks	5	462 ± 181	186 ± 36	124 ± 14	24 ± 4
chicks	11	250 ± 43	189 ± 34	100 ± 57	28 ± 10
χ^2		1.42	0.06	5.16	6.32
df		2	2	2	2
P		NS	NS	.05	.05

Given are means ± standard error. [a)] Tests not computed because most pairs had eggs.

Behaviour as a function of stage in breeding cycle.

Stage in the reproductive cycle was a significant factor affecting variations in flush distance, distance flown from the nest, time to remain near the nest, and distraction display behaviour (Tables 3, 4, Fig. 2). Distraction displays were only given when pipping eggs or chicks were at the nest. Surprisingly, age of the chick did not enter any model as a significant factor affecting nest departure or distraction display behaviour. Thus, whether parents had chicks (as opposed to eggs) entered the models, but age of chick did not. Chicks ranged in age from just hatched (still wet) to fully-feathered and ready to fledge.

Behaviour as a function of being within or outside a seabird colony.

Although all zenaida doves nested on islands with nesting seabirds, not all doves nested within a seabird colony (Table 5). As might be expected,
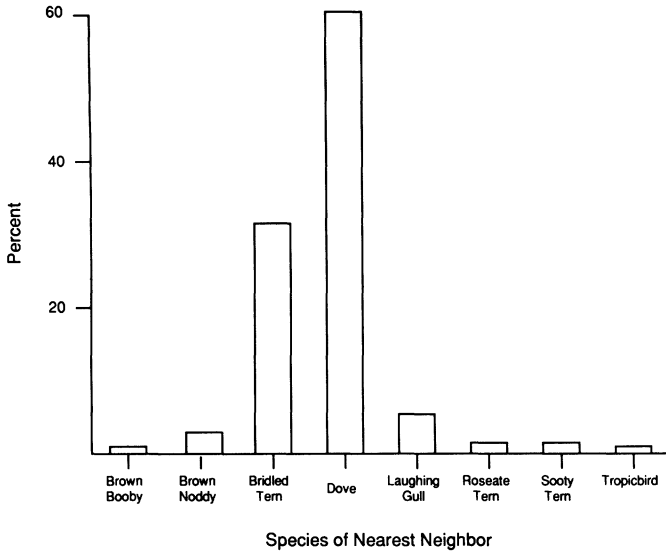
Fig. 3. Nearest neighbor species for zenaida doves as a function of frequency of each species nesting on the islands.

TABLE 5. Behaviour of zenaida doves nesting within or outside seabird colonies

	Nesting within colony	Nesting outside colony	$\chi^2(P)$
Number of nests	97	47	
Nearest neighbor distance (cm)	345.1 ± 28	420 ± 56	3.86 (.05)
Distance to flush (cm)			
eggs	311.1 ± 29	320.4 ± 67	NS
chicks	238.7 ± 57	213.6 ± 38	NS
Distance flown (m)			
eggs	26 ± 2.5	145 ± 11.0	8.03 (.004)
chicks	25 ± 12.0	33 ± 13.0	NS
Time to remain near nest (sec)			
eggs	4.5 ± 2.5	34.5 ± 24.0	4.23 (.03)
chicks	54.5 ± 11.4	67.0 ± 38.1	3.86 (.05)

Given are means ± one standard error. Models are for all data combined.

doves nesting within colonies had closer nearest neighbours than those nesting outside a seabird colony. However, the only variables that varied as a function of location were distance flown during the egg stage, and

time remaining near the nest (Table 5). Doves nesting within seabird col-
onies remained closer to the nest, but remained near the nest for less time
than doves nesting outside a seabird colony.

Behaviour as a function of nesting island.

Flush distance, time remaining near the nest and distance flown from the
nest all varied as a function of nesting island (Tables 2, 3). The distance
we were from the nests when doves flushed was greatest for Yerba, Agua,
Molinos and Lobito, and least for Raton and Geniqui. Time remaining
near the nest was longest for Raton, and least for Geniqui, Matojo,
Yerba and Molinos. The distance flown from the nest was greatest for
Molinos and Raton, and least for Lobito, Matojo and Geniqui. These
differences are attributed in part to habitat and breeding stage differences
(see discussion).

Discussion

Parental investment and offspring vulnerability.

Behaviour during the approach of predators varies depending upon the
nature of the predator and the potential threat it poses to the adults and
reproductive units (eggs or chicks). Parents must balance their own
safety against that of their offspring. Parents that avoid predation during
any one breeding season live to breed in the next breeding season
(WILLIAMS, 1966). Thus, with each predator approach, parents must
decide when to leave the nest, how to leave the nest, and what
antipredator behaviours to perform.

TRIVERS (1972) has proposed that parental investments, including
antipredator behaviour, should increase during the breeding season since
the investment has increased, and the replacement cost of the offspring
is high. Thus, antipredator behaviour should increase through the
season, being highest at the end. CURIO *et al.* (1984) found supporting
evidence for TRIVERS (1972) hypothesis since the strength and risk of nest
defense increased with the age of young in great tits (*Parus major*). How-
ever they only studied pairs with young and did not examine behaviour
of incubating parents.

Others (SKUTCH, 1949; ANDERSSON *et al.*, 1980) have suggested that
antipredator behaviour should relate to the vulnerability of the offspring.
Vulnerability of eggs is lower since the nest is hidden, and the eggs are
silent and motionless. For altricial birds, such as the zenaida dove,
vulnerability of the offspring should be high from hatching until fledging.

Altricial young are particularly vulnerable because they are unable to defend themselves. Thus, a vulnerability hypothesis would predict low risk and little antipredator behaviour during incubation, and increased antipredator behaviour during the brood phase which might involve increasing parental risk.

In this study the behaviour of zenaida doves was consistent with the vulnerability hypothesis, and not with a linear increase in investment. Zenaida doves that were incubating primarily walked several meters from the nest while hidden in the vegetation or rocks, and then flew away. Such behaviour would direct a predator's glance away from the actual location of the nest, and removes the parent from direct physical harm. Once the eggs began to hatch, the parent dove waited until the predator was very close and flew or burst explosively from the nest. Such behaviour also directs the predator's attention from the nest. Distraction display behaviour, where the parent is potentially exposed to the greatest personal risk, occurred immediately during hatching, and was present with brooding parents regardless of the age of the chicks. The age of the chicks did not contribute significantly to the variation in flush distance, time parents remained near the nest, or in the distance parents flew from the nest. However, parents with chicks were more likely to give a distraction display as they flew from the nest than parents with pipping eggs. Our data clearly indicate a change in nest departure and antipredator behaviour at hatching, rather than a gradual shift in parental risk and antipredator behaviour over time. Older chicks were not defended more vigorously than young chicks, suggesting that the vulnerability hypothesis (rather than previous, cumulative investment) is affecting antipredator behaviour of the doves. The vulnerability hypothesis clearly predicts that defense should increase at hatching and remain high until chicks fledge (as happened in this study), whereas the cumulative investment theory predicts defense should increase to hatching, and continue to increase during the chick stage (and it did not in this study).

Predator vulnerability.

Recently KNIGHT & TEMPLE (1986) proposed that the increase in parental defense with season shown by most studies is a result of parental experience with the predator (usually a human intruder). That is, the parent is reinforced for its defense (the intruder leaves without harming adults or young), and so defends more strongly the next time. COLEMAN (1987) subsequently argued that, at best, animals should simply expend the same energy (not more) in defense of the young. He proposed that

parents would not expend more energy for the same result (successful expulsion of the predator). In the present study each nesting dove's behaviour was recorded only once, thus the differences in behaviour we observed as a function of stage in the cycle were not due to seasonality or previous experience with the researchers. Since these islands are legally protected, other people are seldom on the islands, and do not walk through the dense brush where doves nest.

In the islands around Culebra young zenaida doves were once sought as a delicacy. Thus the antipredator behaviour of the parents may be aimed at confusing approaching humans. The explosive, bursting flight of the adult makes it difficult to pinpoint its departure site (the nest). The incubating doves that walk far from the nest before flying insure that the human predators must search a very wide area of dense vegetation, thus decreasing the probabilities of predation. However, close to the nest, the clear white eggs are very visible, and are not cryptic as is the brown back of an incubating parent.

It is not the case that people are "duped" by the distraction display (see ARMSTRONG, 1956), only that it catches the eye, making it difficult to remember where the bird was first observed. Without knowing the initial departure point, it is nearly impossible to locate the nest. This is particularly true in homogenous vegetation or flat rocks without land-marks. It clearly makes the searching task more difficult. We failed to find about 8% of the nests (assuming each dove that departed had a nest), even though we were very experienced.

Other predators that pose a serious threat to eggs and chicks are laughing gulls, hermit crabs (*Coenibita* spp.) and land crabs (*Geocarcinus* sp.) that eat eggs or chicks. Laughing gulls are deterred by the mobbing behaviour of roseate terns and by the difficulty of locating and reaching dove nests in dense vegetation or rock crevices. Such crevices provide no ledges for gulls to land on, and the narrow spaces usually prevent entry by predatory birds. Indeed, there were many nests in rock crevices that we could see but not reach.

Crabs, in our view, provide the most serious threat since we observed them removing eggs and young chicks from nests. Eggs or chicks that are left uncovered can be quickly dragged away by crabs. Eggs are less vulnerable since they must be moved and are not as easily injured. How-ever, we observed crabs injure chicks immediately when they entered a nest. Thus, the rapid return of a parent could save an egg, but might not save an already injured chick. Further, the odors from hatching dove eggs may make it easier for crabs to locate them.

Information parasitism.

NUECHTERLEIN (1981) first suggested that birds may nest in colonies with other species to make use of their early warning and antipredator behaviour. Subsequently, BURGER (1984) showed that grebes that nest with other colonial species have higher reproductive success than solitary-nesting grebes. Thus, we were interested in whether the nest departure and antipredator behaviour of the doves nesting within seabird colonies differed from that of doves nesting outside seabird colonies or on islands with no nesting seabirds.

We did not find doves nesting on any islands that were devoid of nesting seabirds even though the vegetation and rocks seemed suitable. Further, on the seabird islands most dove nests were close enough to nesting seabirds for them to hear the warning cries of the seabirds when humans or other predators approached. Since the doves nest on the ground or in the vegetation or within rock crevices they are usually unable to see approaching aerial predators, but could hear the seabird alarm calls.

In this study distance to flush did not differ in doves that nested within or outside a seabird colony. Although, incubating doves nesting outside a colony flew further away than doves nesting within a colony, there were no differences during the chick phase. Further, doves that nested within a colony remained near the nest for significantly less time than doves nesting outside of the colony. These results suggest that the doves do not alter their flush behaviour, but do alter their own vulnerability. When they nest within a colony they may rely on the mobbing behaviour of the seabirds rather than remain as long to defend the nest.

Breeding phenology.

Breeding phenology differed on the islands. Agua and Raton had pairs with incomplete clutches and pairs with nearly-fledged chicks whereas the other islands had mostly or entirely pairs that were incubating eggs. These differences may relate to the physical location of the islands. Agua and Raton are relatively close to Culebra, and the others are farther away. We frequently observed the doves flying to Culebra to feed during the day. Alternatively, Agua and Raton may be more preferred for nesting.

Summary

1. Zenaida doves (*Zenaida aurita*) nested on several small islands near Culebra, Puerto Rico, under rocks, herbs and low shrubs. When humans approached their nest sites, doves either walked surreptitiously, flew, or burst explosively from the nest when the intruder was very near.

2. Incubating parents usually walked from the nest, parents with hatching eggs usually walked, but sometimes flew from the nest, and parents with chicks usually flew from the nest.

3. Only parents with hatching eggs or chicks gave distraction displays.

4. Variations in flushing distance depended on stage in the reproductive cycle and study island, whereas distance initially flown from the nest also depended on distance to colony edge, and time to remain near the nest also depended on nesting stage and island.

5. Level of nest defense and parental risk increased at hatching, but did not continue to increase with age of the chick. Our data support SKUTCH (1949) and ANDERSSON *et al.*'s (1980) vulnerability hypothesis for parental care rather than TRIVER's (1972) cumulative investment hypothesis.

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