Articles

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Predator–prey interactions between the South Polar skua *Catharacta maccormicki* and Antarctic tern *Sterna vittata*

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Antarctic terns have to co-exist in a limited space with their major nest predator, the skuas. We conducted artificial nest experiments to evaluate the roles of parental activity, nest location and nest and egg crypsis in this simple predator–prey system. Predation on artificial (inactive) nests was higher in traditional nesting sites than in sites previously not occupied by terns, which suggests that skuas memorized past tern breeding sites. Predation on artificial nests in inactive colonies was higher than in active (defended) colonies. Parental defense reduced predation in colonies to the level observed in artificial nests placed away from colonies. This suggests that communal defense can balance the costs of attracting predators to active colonies. Within colonies, predation was marginally higher on experimental eggs put in real nests than on bare ground. Although it seems that the presence of a nest is costly in terms of increased predation, reductions in nest size might be constrained by the need for protective nest structures and/or balanced by opposing selection on nest size. Predation did not differ markedly between artificial (quail) and real tern eggs. A simultaneous prey choice experiment showed that the observed predation rates reflected egg/nest detectability, rather than discrimination of egg types. In summary, nesting terns probably cannot avoid being detected, and they cannot defend their nest by attending them. Yet, by temporarily leaving the nest, they can defend it through communal predator mobbing, and at the same time, they can benefit from crypsis of unattended nest and eggs.

The role of predation risk in the evolution and/or maintenance of avian coloniality is still controversial (Wittenberger and Hunt 1985, Siegel-Causey and Kharitonov 1990, Clode 1993, Kenyon et al. 2007, Sachs et al. 2007, Varela et al. 2007). Nevertheless, currently observed nest predation patterns often suggest an adaptive significance of colonial nesting in terms of increased breeding success. Seabirds, because of their prevalent habit of group living, are a traditional model in studies of costs and benefits associated with colonial breeding (Clode 1993). Seabirds inhabiting species-poor polar areas offer an additional advantage of being relatively simple predator–prey systems, in particular species breeding in the Antarctic area, where they have never been exposed to terrestrial predators.

The largest avian breeding aggregations in the Antarctic are formed by penguins and petrels, whose eggs and chicks are the major terrestrial prey available to the local avian predators – skuas (*Catharacta* spp.; Parmelee 1992, Young 1994, Weidinger 1998, Brooke et al. 1999, Van Franeker et al. 2001). Yet, the comparatively smaller colonies of other Antarctic flying seabirds have received little attention in this respect (Parmelee and Maxson 1974, Kaiser et al. 1988), possibly because they are – from the perspective of the predator (and also researcher) – a negligible prey source (for a review of skua diet see Higgins and Davies 1996). However, from the perspective of less abundant prey species, the impact of predation can be more detrimental than for more abundant and/or large species, where predation is diluted by prey numbers (Brooke et al. 1999, Votier et al. 2004) and may be further reduced through nest defense (penguins; Young 1994) or selection of protected nest sites (some petrels; Varpe and Tveraa 2005).

The Antarctic tern *Sterna vittata* is a circumpolar species breeding on sub-Antarctic islands and the Antarctic Peninsula to 68°S, in loose colonies containing from a few to hundreds of pairs. Both eggs and chicks suffer from heavy avian predation and inclement weather, the overall nest success being generally low and highly variable among geographical locations, years, as well as between colonies within a year (Kaiser et al. 1988, Parmelee 1992, Jabłoński 1995, Higgins and Davies 1996, Casaux et al. 2008). Here, we report on nest predation in the Antarctic tern at the southern border of its breeding range, where the species breeds close to its ecological limits. Terns co-exist here in a limited space with their major avian predator, the South Polar skua *Catharacta maccormicki*.

We conducted artificial nest experiments to evaluate the respective roles of nest site location, nest and egg crypsis and parental activity in the predator–prey interaction between skuas and terns. Nesting terns probably cannot avoid detection by skuas because of their conspicuous behavior and the good visibility of incubating birds against the nest background. Yet, frequent changing of nesting sites between years (Parmelee 1992, Peter et al. 2008) and possibly re-nesting at different sites within a year (Parmelee 1992) suggest some benefit from the abandonment of previous breeding sites. This is to be expected if skuas remember and revisit tern nesting sites once they are discovered. We asked 1) whether artificial nests – without parental activity that may disclose them to skuas – would be preyed upon at a higher rate if they are located in inactive tern colonies compared to sites not previously occupied by nesting terns. We expected 2) that this effect, if present, would increase with distance between the colony and the unoccupied site.

Contrary to attracting predators' attention, breeding terns can actively defend their nests by communally mobbing predators to drive them away from the colony (Parmelee and Maxson 1974, Jabłoński 1995, Whittam and Leonard 2000). We thus also asked 3) whether artificial nests in inactive colonies – without parental defense – would experience higher predation rates than defended nests in active colonies. Because incubating parents temporarily leave their nest to participate in mobbing, the attacking predator has to search for individual unattended nests within a colony. In such cases, cryptic eggs would offer a selective advantage (Blanco and Bertellotti 2002, Sanchez et al. 2004). Because egg coloration may be selectively neutral if predators detect nests before detecting eggs (Götmark 1993), we first asked 4) whether within a colony, experimental eggs placed in real nests would experience higher predation rate than eggs placed on bare substrate. Finally, we asked 5) whether experimental eggs (presumably less cryptic) would experience higher predation rates than real tern eggs, if both egg types are exposed on bare substrate, to exclude any effects of the nest per se.

Material and methods

Field work

The study was conducted at the James Ross Island, NE Antarctic Peninsula (JRI; within ca 13 km of the Johan Gregor Mendel Station: 63°48′S, 57°53′W) during two austral summers – from 1 January to 3 February 2009 and from 3 to 27 January 2011. We mapped the distribution of all breeding birds over ca 117 km^2 of ice-free area of the Ulu Peninsula (for environmental characteristics see Láska et al. 2011). About 340/250 pairs of terns and 38/54 pairs of skuas were breeding in the area during the two study seasons; no penguin colonies are known from this part of JRI (Weidinger and Pavel in press). Although active tern nests in all stages were present throughout the study period, many tern colonies were already abandoned before our arrival. Hence we carefully searched for signs of past nesting in potential breeding sites. The positions of all current-year nests were recorded by GPS and the numbers of adult birds and their activity associated with breeding was recorded throughout the fieldwork.

Active tern nests represented one treatment group in an artificial nest experiments. Artificial nests were baited with Japanese quail *Coturnix japonica* eggs as a surrogate for real tern eggs. The quail eggs were hardboiled and X-ray sterilized just before transportation to Antarctica, to prevent pathogen transmission. These procedures did not influence the external appearance of the eggs. Quail eggs are cryptic (to the human eye), but smaller than tern eggs (32×25 vs 46×33 mm). In addition to quail eggs, we also used a limited number of real tern eggs that we collected from nests that were found already abandoned by the time of our arrival to the study area. All artificial nests contained one egg, completed natural tern clutches contained on average 1.2 eggs (Weidinger and Pavel in press).

We defined the following experimental treatments (Appendix 1). (T1) un-manipulated active tern nests. (T2) quail eggs placed in already inactive real tern nests in abandoned colonies. We used all discovered current-year nests within a particular colony/nest cluster, regardless the size of nest structure. (T3) quail eggs placed on a suitable substrate within inactive colonies. The sites were chosen as to form pairs with T2 nests, separated from each other by a distance of 10 m. (T4, T5) tern and quail eggs, respectively, placed on suitable substrate in an alternating sequence at 10 m intervals; the transects were located < 100 m from the edge of inactive colonies. (T6) quail eggs placed on suitable substrate in transect at 10 m intervals; the transects were located > 1 km from the nearest tern breeding sites (active or abandoned) and about 50 m from an active skua nest. Deployment of artificial nests (T4, T5, T6) in transects was dictated by logistical constraints. Although this spatial pattern differs from that of natural nests, we believe this did not influence foraging behaviour of skuas to a degree that might invalidate the results. We suppose that skuas detect artificial nests one at a time during overflights, not by walking between neigbouring nests. The 10 m interval was chosen as to simulate the inter-nest distance in the core areas of real colonies (for account of nesting densities see Kaiser 1996 and Weidinger and Pavel in press).

The artificial nest treatments T2–T6 were designed to change a particular trait of real tern nests, while keeping the other traits fixed. This allowed a comparison between pairs of treatments (referred to as contrasts C1–C5, hereafter; for definitions see the Appendix 1 and Fig. 1) to evaluate the effect of each particular trait on predation rate. To assess the effect of parental activity (C3), the T2 nests ideally should be compared with same artificial nests located within active tern colonies. However, as we tried to minimize disturbance to active tern nests, we did not place artificial nests within active tern colonies. Hence, we compared artificial T2 nests directly with the active T1 nests. This procedure violates the rule of fixing all but one variable, because these treatments differed not only in the presence of adult birds in the colony, but also in egg type. Hence we inferred the net effect of parental activity from the difference between the composite effect of activity and egg type (C3) and the net effect of egg type (C5).

Both active and artificial nests were inspected in 2–10 d intervals, depending on site accessibility and weather conditions. An active nest was classified as successful (hatched) when a chick was found in or close to the nest, or when faeces around the nest and adult behavior indicated the presence of a chick(s). A nest was classified as depredated if

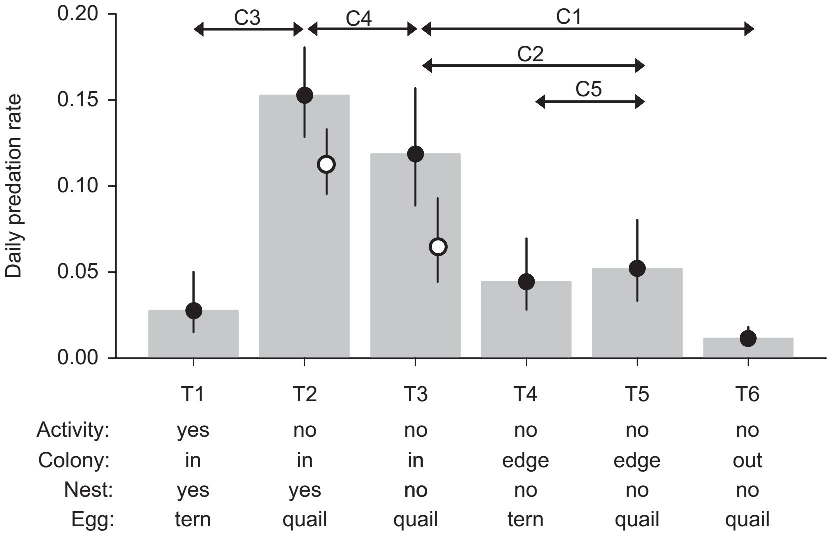

Figure 1. Daily predation rate (with 95% CI) on active Antarctic tern nests (T1) and artificial nests placed in inactive tern colonies (T2, T3), < 100 m from inactive colonies (T4, T5) or > 1 km from colonies (T6). Treatment means T1–T6 are based on a hierarchical analysis that accounts for individual nest samples within treatments. For a full description of treatments, nest samples and analyzed contrast (C1–C5) see Appendix 1. Estimates obtained after excluding two nest samples with the highest predation rates (sample 6 and 9) are shown by open circles.

the egg(s) disappeared before the expected date of hatching, or if we did not find any signs of chick presence. Other sources of mortality (intact frozen eggs, flooding, dead chicks) were treated as censored cases (see below). An artificial nest was considered depredated if the egg disappeared between consecutive nest visits.

To assess whether skuas discriminate between familiar (tern) and novel (quail) egg types and, concurrently, to further validate the use of quail eggs in our nest predation experiment, we performed a simultaneous prey choice test at 10 skua nests in 2011. We placed one tern and one quail egg at a distance of 1.5–2 m from a skua nest within the field of view of the incubating bird. Both eggs were separated from each other by a distance of 0.5 m and were placed on the same substrate (flat stones). The entire setup was monitored by a mini video camera for ≥ 24 h. From the video record we determined the sequence in which the two eggs were eventually contacted/consumed by the skua.

A subset of active tern nests in both years was monitored by mini video cameras to obtain continuous ≥ 24 h records of incubation behavior (unpubl.). As a side product, the video records showed that terns resumed incubation soon (< 3 min) after disturbances by observers, and that none of the nine recorded predation events (all by skuas) was temporally associated with a preceding observer visit.

Data analysis

As the scheduling of nest visits was strongly constrained by weather and logistics, we analyzed nest survival in terms of daily survival rate (DSR). We used the logistic-exposure method (Shaffer 2004) implemented in PROC GENMOD (SAS Inst.), which is an extension of the logistic regression allowing for unequal lengths of nest visit intervals. Each interval between successive nest visits was treated as one observation and the fate of the nest during the interval was the binary response variable (survived/failed). Intervals of uncertain fate or those that failed for reasons other than predation were excluded from the analysis, i.e. the survival record for that nest was censored by the time of the preceding visit. To facilitate interpretation, we converted results from DSR to daily predation rates (DPR).

Each experimental treatment included 2–6 nest samples (colonies or transects), and each sample comprised 18–60 nests, while the effective sample size (= number of survived nest-days + number of nest visit intervals with a predation event; Shaffer 2004) varied from 27 to 666 per sample (Appendix 1). To account for hierarchical structure of the data and unbalanced sample sizes, we estimated treatment means while accounting for the sample effect 'nested' within the treatment effect. Accordingly, we tested differences among treatments as a set of planned contrasts among individual nest samples (Appendix 1). The contrasts C1–C3 (effects of nest site and parental activity) are between independent samples, while the contrasts C4 (effect of nest) and C5 (effect of egg type) are between paired samples (Appendix 1). In addition to test results, we present the effect size expressed as the odds ratio (OR) for daily predation rate. We did not include covariates in the model. The factors considered important a priori were controlled by the experimental design, and we believe that the potential effects of unknown factors were randomized by spatial and temporal interspersion of treatments among nest samples. We could not evaluate interactive effects because, owing to logistical constraints, our experiment was not designed to be factorial.

Results

Daily predation rate varied markedly among the experimental treatments (Wald $\chi^2_5 = 152.5$, $p < 0.001$; Fig. 1,

Appendix 1) as well as among samples within treatments (Wald $\chi^2_{14} = 101.4$, $p < 0.001$; Appendix 1). DPR on active tern nests was higher in 2009 than in 2011 (Appendix 1), though the limited sample size and the lack of replication precluded any formal analysis.

Predation on artificial nests was remarkably higher in inactive colonies than in unoccupied sites far from a colony (C1; OR = 11.49, CI: 6.56–20.14; Wald $\chi^2_1 = 72.77$, $p < 0.001$), and higher than in unoccupied sites close to a colony edge (C2; OR = 2.45, CI: 1.39–4.32; Wald $\chi^2_1 = 9.57$, $p = 0.002$). Predation on artificial nests in inactive colonies was markedly higher than predation on active tern nests (C3; OR = 6.36, CI: 3.30–12.25; Wald $\chi^2_1 = 30.59$, $p < 0.001$). The comparison of paired samples showed that predation on quail eggs was marginally higher if they were put in real nests rather than on bare ground (C4; OR = 1.61, CI: 1.01–2.55; Wald $\chi^2_1 = 4.06$, $p = 0.044$), and that predation tended to be marginally higher on quail eggs than on real tern eggs, though the difference was far from significant (C5; OR = 1.24, CI: 0.71–2.16; Wald $\chi^2_1 = 0.55$, $p = 0.458$). Reanalysis after excluding two 'outlying' nest samples with the highest DPR (Appendix 1: samples 6 and 9) revealed effects of the same direction, but of smaller size (Fig. 2); the difference in DPR between a colony and its edge was no longer significant (C2; OR = 1.25, CI: 0.68–2.31; Wald $\chi^2_1 = 0.53$, $p = 0.468$).

Of the 10 replicates of prey choice test, skuas either consumed (9 cases), or ignored (1 case) both experimental eggs. If the eggs were consumed, neither the sequence of first contact with an egg (5 × tern vs 4 × quail) nor the sequence of egg consumption (6 × tern vs 3 × quail) suggested a clear-cut discrimination between egg types (note that for the given sample size, the inequality would have to be at least 8 vs 1 to be significant at $p < 0.05$).

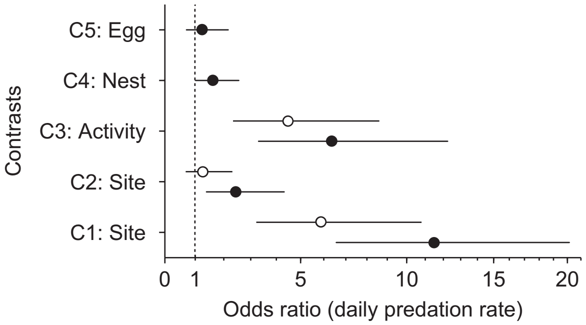

Figure 2. Effect sizes, expressed as the odds ratio, resulting from analyses of contrasts between nest treatments. C1: inactive colonies vs non-breeding sites > 1 km from colonies; C2: inactive colonies vs non-breeding sites < 100 m from colonies; C3: inactive colonies vs active colonies; C4: real nests vs bare ground at paired random sites; C5: quail eggs vs tern eggs. See Fig. 1 for treatment means and Appendix 1 for descriptions of nest samples and definitions of contrasts. Estimates obtained after excluding the two nest samples with the highest predation rates (sample 6 and 9) are shown by open circles.

Discussion

We found that predation rate by skuas varied among locations according to their past occupation by nesting terns. Predation on artificial nests was much higher in inactive tern colonies than in similar sites outside colonies, and this effect increased with distance from the colony (Fig. 2: C1 and C2). This effect cannot be accounted for by differences in tern activity (breeding terns were absent from either site by the time of the experiment) or local nest density (mean ≤ 1.4 nest 100 m^{-2} in largest clusters of nests within colonies [Weidinger and Pavel in press] vs ~ 1 artificial nest 100 m^{-2} outside colonies). The remarkably high predation in past tern colonies (Fig. 1: T2 and T3) suggests that skuas memorized tern breeding sites and continued to revisit them in search for prey, even weeks after their abandonment. In contrast, the very low predation rate in sites not previously occupied by terns (Fig. 1: T6) likely resulted from random encounters with nests, rather than from intentional searches for prey. An intermediate predation rate in sites outside but close to past tern colonies (Fig. 1: T4 and T5) may reflect a higher probability of random encounters in sites close to areas of increased foraging activity. All this suggests that skuas do not search directly for nests over the whole snow-free area, but concentrate their foraging activity to currently active (disclosed by parental activity) and past (memorized) tern breeding sites. While it seems that active tern nests ultimately cannot avoid detection by skuas, changing nesting sites (Parmelee 1992, Peter et al. 2008) still may provide a survival advantage, if skuas divide their nest-searching effort between active and past colonies, and/or if skuas switch to active colonies after some delay.

We found strong support for an effect of parental colony defense – predation on artificial nests in abandoned colonies was markedly higher than predation on active tern nests (Fig. 2: C3). While nests in inactive (not defended) colonies were highly vulnerable (Fig. 1: T2 and T3), parental defense could reduce predation rate in active colonies to the level observed in artificial nesting sites away from colonies (Fig. 1: T1 vs T6). This suggests that parental defense can balance the cost of predator attraction to active colonies. Although the anti-predatory significance of nest position within a colony is well documented in several tern species (Becker 1995, Brunton 1997, Hernandez-Matias et al. 2003, Silva et al. 2010) and seabirds in general (Wittenberger and Hunt 1985), it remains to be determined whether communal defense by tern colonies may outweigh the potential benefit of inconspicuous solitary nesting away from traditional colony sites (Kenyon et al. 2007). Although even solitary nesting would probably not remain undetected in the simple polar habitat, solitary nests may still benefit from being an unattractive prey, in particular if skuas increase their foraging effort with local prey numbers (Müller-Schwarze and Müller-Schwarze 1973, Emslie et al. 1995).

Although skuas seem to have good knowledge of current as well as past tern breeding sites, they still have to use some other cues to locate individual nests within a colony. When approached by a predator, incubating terns take off to engage in mobbing, thus leaving their nests unattended. The number of rapid (presumably forced) take-offs seen on video records of incubated nests (ca 1.2 take-offs h^{-1}; unpubl.) suggests that attacks are frequent. Skuas must either remember the position of incubating terns before flushing them, and/or search directly for the eggs. In either case, attacks have to be short (because of mobbing) and cryptic nests and eggs would make detection less likely.

Antarctic tern nests in the southern parts of the breeding range vary from being placed on bare ground or a shallow scrape in soft substrates to mounds made of small stones (Jabłoński 1995, Higgins and Davies 1996, Kaiser 1996). We found that experimental eggs put in real nests of the latter type suffered from marginally higher predation rate compared to eggs placed on bare ground. Because the eggs in both site types were not attended by adults, the differential predation could not be an effect of skuas' short-term memory of nest position, but rather a result of direct searches. This suggests that the minimization of nest size would provide a selective advantage in terms of reduced predation rate, but this is likely constrained by the need for some nest structure keeping the egg(s) in place and protecting them from flooding (Jabłoński 1995, Fargallo et al. 2001). We can only speculate as to why nests seem to be considerably larger (i.e. more conspicuous) than may be necessary for egg protection – the cross-sectional area of a single tern egg (ca 11.3 cm^2) is only about 5.5% of the area covered by a typical mound of stones (mean $= 235 \pm 12$ SE cm^2, max $= 490$ cm^2, n $= 57$ nests). Although we cannot distinguish among the range of alternative explanations (e.g. sexual selection on nest size; Soler et al. 1998, Fargallo et al. 2001), of note are two side findings related to nest size. First, incubating birds exhibited nest-building behavior throughout the incubation period, and such behavior was most frequent just before/after change-overs between partners (own video-based data; see also Parmelee and Maxson 1974, Kaiser 1996). Second, nests containing two-egg clutches were marginally larger than nests with one-egg clutches (mean difference $= 56 \pm 33$ SE cm^2).

Similar to many other ground-nesting birds with inconspicuous nests (Götmark 1993), the eggs of the Antarctic tern are remarkably cryptic, at least to the human eye. Our finding that predation did not differ markedly between quail and tern eggs validates the use of quail eggs as a surrogate for real tern eggs to measure relative predation rates. The result of the simultaneous prey choice experiment suggests that the predation rates found in an artificial nest experiment resulted from egg/nest detectability, rather than from egg discrimination based on coloration (Montevecchi 1976a), size (Montevecchi 1976b), or overall prey novelty (Müller-Schwarze and Müller-Schwarze 1973).

The effects of nest size and egg type, if real, were too small to seriously bias or even reverse the effects of parental activity and nest site (Fig. 2). As these results were also robust against outlying data samples (Fig. 2), we conclude that our focal tests were not biased by the artificial nest experimental design or the data included, and that the effects of parental activity and nest site reported here are real.

Altogether, this study has demonstrated the anti-predatory value of multiple nesting characteristics in a simple avian predator–prey system. Under the constraints imposed by the polar habitat, where terns and skuas are forced to co-exist in a limited snow-free area, Antarctic terns seem to have developed an efficient strategy for breeding in the presence of their major avian nest predator (Parmelee 1992). Nesting terns, either colonial or solitary, probably cannot avoid being detected, and they cannot defend their nests by attending them. Yet, by temporarily leaving the nest, they can defend it through communal predator mobbing, and at the same time, can benefit from the crypsis of unattended nests and eggs.

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Appendix 1

Descriptions of experimental treatments, nest samples and comparisons among them in a study of nest predation in the Antarctic tern.

Treatment	Active[a]	Colony[b]	Nest[c]	Egg[d]	Sample[e]	Year	n[f]	DPR[g]	95% CI	C1[h]	C2	C3	C4	C5
T1	yes	in	yes	tern	1	2009	43, 331	0.0452	0.0278–0.0725			+		
					2	2011	26, 168	0.0167	0.0054–0.0505			+		
T2	no	in	yes	quail	3	2009	60, 611	0.0913	0.0716–0.1156			−		
					4	2009	55, 176	0.2040	0.1572–0.2603			−		
					5	2009	21, 189	0.1037	0.0685–0.1539			−		
					6	2009	18, 27	0.5078	0.3276–0.6859			−	+	
					7	2011	26, 155	0.1063	0.0686–0.1611			−	+	
					8	2011	25, 161	0.0857	0.0522–0.1373			−	+	
T3	no	in	no	quail	9	2009	20, 48	0.3387	0.2261–0.4731	+	+		−	
					10	2011	26, 159	0.0883	0.0546–0.1396	+	+		−	
					11	2011	25, 225	0.0467	0.0260–0.0823	+	+		−	
T4	no	edge	no	tern	12	2009	28, 442	0.0396	0.0250–0.0619					+
					13	2011	23, 109	0.0498	0.0225–0.1067					+
T5	no	edge	no	quail	14	2009	28, 421	0.0503	0.0333–0.0752		−			−
					15	2011	24, 100	0.0539	0.0243–0.1150		−			−
T6	no	out	no	quail	16	2009	30, 666	0.0089	0.0039–0.0196	−				
					17	2011	29, 305	0.0311	0.0168–0.0568	−				
					18	2011	38, 430	0.0270	0.0153–0.0469	−				
					19	2011	31, 391	0.0051	0.0012–0.0200	−				
					20	2011	32, 373	0.0053	0.0013–0.0211	−				

[a] yes = active natural nests, no = artificial nests.

[b] in = within colony, edge = close to colony (< 100 m), out = far from colony (> 1 km).

[c] yes = real nest, no = bare ground: either random site 10 m apart from paired real nest (T3), or sites in transects at 10 m intervals (T4, T5, T6).

[d] tern = real eggs in active nests (T1) or real eggs collected from abandoned nests (T4), quail = Japanese quail eggs.

[e] samples 6–8 were paired with samples 9–11 (representing the same three colonies); samples 12–13 were paired with samples 14–15 (representing the same two transects of artificial nests).

[f] number of nests and effective sample size (= number of survived nest-days + number of observation intervals during which a nest was depredated).

[g] daily predation rate.

[h] contrasts among nest samples employed in tests of treatment effects: colony (C1, C2), activity (C3), nest (C4), egg (C5).