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Original Article

Deceiving predators: linking distraction behavior with nest survival in a ground-nesting bird

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Individual behavior that minimizes predation risk is favored by natural selection. Ground-nesting birds employ different defensive behaviors as part of their antipredator strategies because they nest where a wide range of predators have access. We investigated the influence of distraction displays on breeding success in the Kentish Plover, *Charadrius alexandrinus*, in order to explore the role of the defensive behavior on nest survival. We quantified the intensity of defensive behavior of adult plovers in response to nest disturbance caused by an approaching researcher, by ranking display types according to the intensity and exposure to predation. We also examined sex differences in nest defense to determine whether the existence, intensity, and consistency of individual defensive behaviors could have an impact on nest survival. We used the nest survival model in Program MARK to estimate daily survival rates of nests and to examine the influence of temporal, behavioral, and habitat variables on nest success. Our results show a positive correlation between male and female defense behaviors within pairs and that nests in which parents invested more on defense survived longer. Nevertheless, there were differences in the risks assumed by the 2 members of breeding pairs in nest defense, with females performing riskier defensive behaviors than males. The top-ranked nest survival models included combined additive effects of site, season, habitat type, nest exposure, and the defense behavioral response of females as best predictors. Finally, our study highlights that increased risk assumption in offspring defense is advantageous in terms of individual fitness.

Key words: ***Charadrius alexandrinus*, defense investment, distraction displays, MARK, plovers, predation risk.**

INTRODUCTION

Animals avoid predation through different adaptations and strategies such as early predator detection, cryptic coloration, or flushing behavior (Magnhagen 1991; Koivula and Rönkä 1998; Colwell 2010). As a consequence, individual behavior that minimizes predation risk is favored by natural selection (Lima and Dill 1990). From the prey perspective, defensive tactics are either based on fleeing or remaining motionless (Lima and Dill 1990). Nevertheless, despite the obvious advantages of flushing behavior (Burrell and Colwell 2012), potential preys may approach their predators for different reasons (Dugatkin and Godin 1992). For instance, birds may thus proceed so as to evaluate the actual threat posed by predators (predator risk assessment), and act accordingly. In general, predator approaching increases the chances of being preyed upon and thus, this behavior can only be understood from a cost–benefit perspective (Dugatkin and Godin 1992), with parental offspring defense being one of the most prominent examples of this paradoxical behavior (Anderson et al. 1980).

Some birds have developed particular modalities of parental defense based on performing displays with the aim to divert predator attention from offspring (Gochfeld 1984; Sordahl 1986; Caro 2005; Colwell 2010) and direct it towards fake nests or easy preys. This can be achieved through the display of dishonest signals concerning their physical condition or by mimicking a reduced ability to escape. Given that this defensive behavior is costly (Brunton 1986; Sordahl 1990a), birds are expected to trade-off the burden of a higher predation risk for increased offspring survival (Montgomerie and Weatherhead 1988; Dugatkin and Godin 1992; Frid and Dill 2002).

The behavior of incubating birds has a significant impact on breeding success. Previous studies have shown that certain adult behaviors (e.g., flushing behavior of incubating adults or the frequency of incubation recesses) are clearly linked to a decrease in predation risk of both adult and nests (Koivula and Rönkä 1998; Amat and Masero 2004a; Smith et al. 2012; Gómez-Serrano and López-López 2014). Nevertheless, the impact of the defensive

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behavior on the breeding success has received little attention so far (Caro 2005; Smith and Wilson 2010). Moreover, the inclusion of these behavioral variables into nest survival models remains unexplored (Colwell et al. 2011).

Ground-nesting birds' nests are accessible to a wide range of predators. Therefore, it is expected that defensive behaviors will play a major role in nest survival (Gochfeld 1984; Montgomerie and Weatherhead 1988; Rytkönen 2002). Shorebirds employ different types of defensive behaviors as part of their antipredator strategies (Gochfeld 1984; Sordahl 1986; Larsen 1991; Colwell 2010), performing both distraction displays as well as aggressive mobbing (Simmons 1955a; Jónsson and Gunnarsson 2010). To address the role of the defensive behaviors on nest survival, we explored the influence of distraction displays on breeding success in a ground-nesting bird, the Kentish Plover, *Charadrius alexandrinus*. To this end, we quantified the intensity of defensive behavior of adult plovers in response to nest disturbance caused by an approaching researcher. We also examined differences in nest defense within breeding pairs to determine whether the existence, intensity, and consistency of individual defensive behaviors have a significant impact on nest survival. Finally, we included the defensive behavior of adults in nest survival models at the same level as habitat covariates, with the aim to explore the relative contribution of these behaviors on nest success.

Specifically, we tested whether 1) investment in nest defense differs between males and females within pairs; 2) nest survival is correlated with the intensity and frequency of defensive behavior exhibited by one or both members of the pair; and 3) nest survival models that take into account variables of defensive behavior fit better than those that only include environmental variables.

MATERIALS AND METHODS

Study species

The Kentish Plover is a ground-nesting shorebird distributed along Eurasia and Africa (BirdLife International 2015). Kentish Plovers may breed in different habitats throughout their range, including coastal beaches, river banks with pebbles, sand bars, salt pans, and salt flats (Fraga and Amat 1996; Oltra and Gómez-Serrano 1997; Colwell et al. 2005). Sandy beaches are an important natural breeding habitat for Kentish Plover, but beaches are also highly valued by humans for recreational purposes. The study species is listed as threatened in the Valencian Community (Eastern Spain) since 2013 where this study has been conducted. Along the Mediterranean coast of Spain, its population decline is attributed, at least partially, to habitat degradation associated with an increase of human disturbance (Oltra and Gómez-Serrano 1997; Figuerola and Amat 2003; Figuerola et al. 2005). Kentish Plover exhibits biparental incubation, with females and males usually incubating during the day and at night, respectively (Fraga and Amat 1996; Kosztolányi and Székely 2002; Kosztolanyi et al. 2003; Amat and Masero 2004b). Predation is one of the major causes of nest failure (Fraga and Amat 1996; Norte and Ramos 2004; Saalfeld et al. 2011; Gómez-Serrano and López-López 2014). In the studied beaches, predation affects from 6% to 25% of nests initiated (Serradal 6%; Almenara 25%; Punta 20%), and the main predators are the Yellow-legged Gull (*Larus michahellis*) and mammals (especially hedgehogs, *Erinaceus europaeus*) (authors unpublished data). Nesting plovers usually perform a variety of distraction displays as part of their antipredator strategies (Simmons 1951; Cramp and Simmons 1983).

Study area

We sampled 3 beaches in the Castellón and Valencia provinces (Eastern Spain): Serradal (Castellón de la Plana, 40° 00′ N, 0° 01′ E), Almenara (39° 43′ N, 0° 11′ W) and Punta (Valencia 39° 18′ N, 0° 17′ W). All 3 sites have natural dune vegetation. Punta (1.2 km in length) and Serradal (1.1 km) are natural sandy beaches, whereas Almenara (2.3 km) is a natural beach of mixed sandy areas with gravel and pebbles. The 3 coastal areas benefit from different types of legal protection according to European and regional legislation. At these 3 sites, Kentish plovers nest primarily on embryonic shifting dunes and annual vegetation of drift lines, but also in grasslands of small annual plants that grow on deep sandy areas among dry interdunal depressions (Gómez-Serrano and López-López 2014). Dominant plants within these habitats include *Elymus farctus*, *Ammophila arenaria*, *Medicago marina*, *Lotus creticus*, *Otanthus maritimus*, *Pancratium maritimum*, *Sporobolus pungens*, and *Cakile maritima* (Gómez-Serrano and López-López 2014).

The 3 beaches are subject to different intensities of human disturbance. Serradal is a beach frequented by people for leisure (>10 people/km/h; authors' unpublished data). On the other hand, Almenara has an intermediate level of human disturbance, with lower human presence as compared to Serradal (1–5 people/km/h; authors' unpublished data). Finally, Punta is a bird sanctuary with restricted access, where human presence is almost negligible (managers and occasional trespassers) (Gómez-Serrano and López-López 2014).

Field procedure

Our study was conducted during 2 different periods. Firstly, we carried out research at Serradal between 1993 and 2001, during each breeding season; secondly, between 2007 and 2008 at the 3 study sites simultaneously. The same observer recorded all data across study areas and years, so there was no bias due to variability among observers.

Kentish plover nests were found by systematically searching beaches and dune systems from early March to late July. Once a nest was found, it was individually geolocated (i.e., including GPS location and a brief schema of close vegetation and objects) and visited every 3–5 days to monitor nest fate. We marked each egg so as to identify it during subsequent visits and to record egg-turning activity. There were no differences in the rate of nest visits across years and study sites. Kentish plovers were not marked in this study.

Nest fate

Nests were considered successful when at least 1 egg hatched. Evidence of hatching included the presence of 1) chicks; 2) eggshell evidence (i.e., small fragments of detached eggshell membranes in nest scrape) (Mabee 1997; Mabee et al. 2006) or 3) adults with chicks or adults performing distraction displays when nests scrapes were empty close to hatching date. Evidence of predation included 1) partially consumed eggs in nests scrapes or their surroundings, 2) presence of a mixture of yolk and sand from broken eggs, or 3) the disappearance of eggs before expected hatching date.

The absence of adults in the vicinity of the nest and the lack of response from nesting birds (i.e., distraction displays), were important aspects of this study. Therefore, we carefully monitored nest activity during each visit. We considered that nests were active when they were attended by adults for incubation tasks. Evidence of nest activity included the observation of: 1) incubating parents; 2) incubating parents flushing from the nest when the observer approached;

3) adults performing distraction displays against potential predators (including researchers) in the vicinity of the nest; 4) egg-turning since the previous visit; 5) normal development according to the egg-flotation schedule (Mabee et al. 2006); and 6) a high density of plover footprints on the sand around the nest scrape. Egg-turning activity was monitored by 2 measurements: egg position and rotation. To this end, eggs were individually marked in its central part the first time they were found, and the position of the mark was recorded every visit. In each control, we took a photograph of the nest (geographically oriented) and we recorded the position of each egg. We use these photographs to check for changes in the position and angle of the eggs within the nest between consecutive visits. The movements of eggs obtained by both methods were used as evidence that nests were active, given the frequency with which they were rotated by parents during incubation. We considered that nests were deserted if there was no evidence of the formerly described signs of activity, confirming this fate on subsequent visits. For failed unsuccessful nests, we assumed that either predation or desertion had occurred halfway between the last visit when nest activity was recorded and the subsequent one, when no activity was observed.

We assessed laying date according to clutch size and laying interval for the Kentish Plover (Fraga and Amat 1996; Colwell 2006; Page et al. 2009). We assumed that nests with 1 egg had been initiated on the same day they were encountered, whereas those with 2 eggs and a third one observed in the following visit were considered to have been started the day before. Laying date in nests with complete clutches (i.e., with 3 eggs, the modal clutch size, or 2 eggs without a third one on a subsequent visit) was estimated using the hatching date or through the egg-flotation pattern (Van Paassen et al. 1984; Mabee et al. 2006). Alternatively, when the laying date was unknown (i.e., the nest was found with complete clutch) but the Plover's courtship scrape was previously recorded (Muir and Colwell 2010), we assumed that laying date had taken place halfway between the last visit with the empty nest scrape and the following visit with complete clutch.

For each nest, we calculated survival rate as the number of days elapsed since the laying of the first egg until the hatching of last egg, or until predation or desertion. The average maximum number of days that nests typically survive is 31 (Amat and Masero 2004a).

Habitat measurements

We recorded nest locations using a handheld Global positioning system (GPS). Subsequently, we corrected the coordinates with an ortho-rectified aerial photograph with the images loaded into GIS software. This procedure allowed us to precisely assess nest distance to the seashore. For this purpose, we used different aerial photographs of study sites, in an attempt to achieve a match as close as possible between the year images were taken and the date of nest inventory. Each nest was assigned to one of the following habitat types as described by Gómez-Serrano and López-López (2014): 1) tidal debris (i.e., beach area outside the tidal zone where scattered organic and inorganic remains washed by the sea accumulate; 2) embryonic shifting dunes (i.e., first stages of dune build-up, consisting of sand ripples or raised sand bars on the upper parts of the beach); 3) shifting dunes (mobile dunes forming seaward dunes, typically following embryonic shifting dunes); and 4) semi-fixed dunes (i.e., dunes with a low relief at the rear of shifting dunes with vegetation dominated by geophytes and small-sized scrubs). We assigned nests located in grasslands of small annual plants that grow on deep sand areas among dry interdunal depressions to the latter habitat type.

Plovers tend to nest on bare sites in order to enhance early detection of predators (Burger 1987; Amat and Masero 2004a; Muir and Colwell 2010; Saalfeld et al. 2011; Gómez-Serrano and López-López 2014). On sandy beaches, such environments are usually found between the seashore and the first shifting dunes. This is an area more exposed to adverse weather events (e.g., sea storms, flooding, etc.) but also to the sea breeze, which may have a cooling effect that alleviates heat stress on eggs and incubating adults (authors' unpublished data). In order to evaluate the influence of these environmental factors on nest survival, the degree of nest exposure was assigned to 2 categories: exposed nests (i.e., unprotected nests usually lying within tidal debris, embryonic shifting dunes, shifting dunes, and interdunal corridors); unexposed nests (i.e., protected nests usually located within semi-fixed dunes and interdunal depressions). We also recorded the substrate type for each nest site and classified it as sand or pebbles. We included substrates consisting of a sand and pebble mixture in the latter category. Finally, we added a binary covariate of management based on the presence or absence (i.e., bird sanctuary) of human disturbance at study sites.

Nest defense

Typically, Kentish plover distraction behavior consists of 2 components. Initially, when a potential predator approaches the nest, the incubating adult crouch-runs away with legs bent, neck depressed, and body horizontal to the ground in order to go by unnoticed (Simmons 1951). Subsequently, if predation risk persists, adults may perform distraction displays to lure the predator away from the nest (Cramp and Simmons 1983).

In this study, distraction behavior of adult plovers was recorded in response to nest disturbance caused by an approaching researcher. We walked in a straight line towards the nest from a distance of 150 m at constant speed (50 m/min), in order to avoid the bias associated with flush initiation distance (Blumstein 2003). When the incubating adult left the nest, we recorded its behavior and monitored both parents separately as we approached the nest. Once we reached it, we stood close to the nest for 2 min, during which we recorded birds' behavior. Subsequently, we recorded habitat and nest characteristics and, after that, we walked away.

We ranked display types from little to extreme on a subjective scale according to the intensity (i.e., energy expenditure) and exposure to predation (Sordahl 1986; Bruntom 1990; Pavel et al. 2000). Both sexes, sexed by differences in plumage characteristics, were scored on an ordinal scale ranging from 0 to 6, with higher values reflecting greater proximity (i.e., higher exposure to predators) and higher intensity of defense (Brunton 1990; Møller 1984; Lord et al. 2001; Møller and Nielsen 2014). For each nest approach, we only used the highest value of the ranked behavior for each parent for subsequent analysis.

Defensive behaviors may be increased in frequency and (or) intensity as predators approach offspring (Byrkjedal 1989; Caro 2005). Moreover, displays performed closest to predators involve greater predation risk (Lima and Dill 1990). For these reasons, we considered the distance between the bird and the observer to categorize behavioral variables (Table 1).

We repeated nest approach experiments on separate days during the incubation period (Table S1, Supplementary Material). To avoid a possible cumulative effect of humans' presence on the bird's behavior, we only considered data from nests that had not been previously visited by us on the same day, and when humans had not been observed in the vicinity of the nest for at least 1 h before the experiment. For the same reason, we separated nest approaches at least 3 days to minimize habituation to standardized disturbance stimuli (Gochfeld 1984; Yasué and Dearden 2006; Muir and Colwell 2010).

Table 1

Ranked distraction behaviors of breeding Kentish Plovers in response to nest disturbance caused by an approaching researcher

Ranked response	Intensity of display	Summary behavior
0	Bird absent or early departure, without recorded return during the visit	Absent
1	Bird leaves the nest and flies to the shore or to an open site within its territory, from where it feeds or rests, but pays no further attention to the researcher	Present
2	Bird flies or runs away, stopping at some distance (usually more than 15 m) and watches the researcher from a place with good visibility	Vigilance behavior
3	Bird flies over or around the researcher and emits alarm calls	Flight alarm calls
4	Bird approaches the researcher (usually closer than 10 m) emitting alarm calls	Ground alarm calls
5	Bird performs one of the following mobile distraction displays at a distance closer than 10 m from the researcher: mobile lure display with wings beating the ground (Simmons 1951); incubation feigning (i.e., the bird runs and then crouches onto the ground to simulate incubating or brooding duties; Gochfeld 1984; Caro 2005); rodent-run; simulating being injured bird (e.g., mobile broken-wing display) (Cramp and Simmons 1983; Gochfeld 1984; Bergstrom 1988)	Mobile distraction displays
6	Bird performs one of the following stationary lure displays at a distance closer than 10 m from the researcher: bird lies on ground while beating wings slowly; bird lies motionless while keeping its wings extended as if exhausted or shuffling wings spasmodically; bird lying while beating wings repeatedly rhythmically or spasmodically (Simmons 1951; Cramp and Simmons 1983)	Stationary distraction displays

Distraction displays usually start upon completion of egg-laying, although some birds perform low intensity and risk displays during nest-scrape stage (e.g., vigilance behavior or ground alarm calls). In this study, we only used the recorded behavioral displays once nests had complete clutches. To account for a potential effect of parents' investment in defensive behavior with increasing nest age, we conducted a preliminary test between male and female-ranked behavior against nest age (measured as days since the first egg is laid). Since there were several approaching experiments per nest, we randomly selected data of one approaching experiment per nest to avoid pseudoreplication. These tests showed no relationship between nest age and defensive behavior (Spearman rank correlation; male: $r_s = 0.003$, $N = 225$, $P = 0.959$; female: $r_s = 0.002$, $N = 225$, $P = 0.980$). Additionally, in order to account for variations in distraction behavior during the day, we conducted experiments in the morning and in the afternoon on separate days.

Data analysis

We used the nest survival model (Dinsmore et al. 2002; Dinsmore and Dinsmore 2007) provided in Program MARK, version 8.0 (White and Burnham 1999) to estimate daily survival rates (DSR) of nests and to examine the influence of temporal (e.g., year, time of the nesting season [NS], and nest age with respect to NS start), behavioral (nest defense), and habitat variables on nest success.

Four input data are required to build the encounter histories for each nest in Program MARK nest survival analysis: 1) day of the NS in which the nest was found; 2) the last day the nest was active; 3) the day the nest was checked for the last time; and 4) nest fate (0 = successful, 1 = failed) (Cooch and White 2014). We linked each encounter history with covariates expected to influence nest survival (Table 2). The covariates included the following: habitat type, distance to the seashore, substrate type (binomial), degree of exposure (binomial), and human disturbance (binomial). Each encounter history also included covariates for year and site.

Our interest was to explore the existence of a possible link between parental defensive behavior and nest survival while taking into account the cumulative contribution of these behaviors during the incubation period. To achieve this goal, we analyzed the set of different records of ranked behaviors, which we obtained during our visits to nests. We used the ranked response to create a subset of 10 new variables so as to integrate them into survival models (Table 2). In species with biparental care, it is essential to consider the defensive behavior of both members to assess the impact on reproductive success (Burtka and Grindstaff 2015). Accordingly, we considered the additive effect of defensive behavior exhibited by both sexes through the integration of the ranked responses of males and females in different single variables for each nest.

We ranked a set of candidate models and compared them using Akaike's Information Criterion (Akaike 1973) corrected for small sample sizes ($\mathrm{AIC_c}$). We used $\Delta\mathrm{AIC_c}$ values and their relative normalized weights (w_i) to provide evidence of the relative support for each model (Burnham and Anderson 2002). We assessed the importance of the covariates included in the top-ranked models using beta estimates with standard errors and 95% confidence intervals (CI) provided by Program MARK. Each covariate was considered as biologically informative if confidence intervals did not overlap 0. Annual estimates of nest success for each site were calculated by multiplying DSR to the 31st exponent, consistent with the average maximum number of days that nests typically survived (Amat and Masero 2004a).

We used a hierarchical model selection approach to identify the optimal predictive model based in a 4-stage modeling procedure (Sexson and Farley 2012) (Table 2). We identified the model that best fitted the data in each state, by assessing every additive combination of different covariates of the same type. For each stage, the best-fitted model was used for the next stage of model building.

Firstly, we started model building with the simplest model, assuming that all nests had the same DSR every day (i.e., a constant DSR over time). Secondly, we fitted models to assess the relationship between DSR and time, considering linear trend (T), and quadratic trend (TT). At this stage, we included effects of year, site, and management (human disturbance). In the second stage, we incorporated the effects of nest age (days) relative to the start of the NS, year, and site. Thirdly, we added the effect of nest age (days) in the day of the first encounter since the beginning of the incubation period. In the fourth stage, we added habitat covariates (habitat type, substrate, distance to the seashore, and degree of exposure). In the final stage, we added the behavior covariates of adults to the best model of the previous stages. We did not evaluate the additive effects of the behavior of 1 sex (male or female) simultaneously with variables describing total nest behavior (i.e., those including the behavior of male and female jointly). The influence of each additive covariate in each candidate model was assessed using the 95% CI provided by Program Mark (Burnham and Anderson 2002). No goodness-of-fit

Table 2

Description of the covariates related to habitat, season and behavior of plovers used in the nest survival models. The stage of the hierarchical modeling process in which the covariate is used is shown in the first column

Modeling stage	Abbreviated covariate	Description
1	Site	Serradal, Almenara, and La Punta beaches
1	Year	Breeding season
1	Management	Human disturbance (1/0)
2	Nest_season	Nest age (days) on the first day of the NS (see Cooch and White 2015 for more details)
2	Nest_age	Nest age (days) in the day of the first encounter since the beginning of the incubation period (see Cooch and White 2015 for more details)
3	Exposure	Nest exposure (1/0)
3	Seashore	Distance (m) to the seashore
3	Habitat	Habitat types
3	Substrate	Substrate types (1/0)
4	Male_behav	Average value of all records for male ranked behavior ranging from 0 (minimum value of nest defense) to 6 (maximum value)
4	Female_behav	Average value of all records for female ranked behavior ranging from 0 (minimum value of nest defense) to 6 (maximum value)
4	Nest_behav	Average of the maximum value of nest defense recorded for the male and the female in each visit (i.e., ranging from 0 to 6)
4	Total_nest_behav	Average value of all records for male and female ranked behavior (i.e., from 0 to 12)
4	%Male_behav	Percentage of male ranked behavior values higher than 2 (i.e., thus assuming higher risk)
4	%Female_behav	Percentage of female ranked behavior values higher than 2
4	%Nest_behav	Percentage of nest ranked behavior values higher than 2 (the maximum value recorded during each visit for the male or the female was used)
4	Max_ Male_behav	Maximum value of male ranked behavior
4	Max_ Female_behav	Maximum value of female ranked behavior
4	Max_ Nest_behav	Maximum value of nest ranked behavior (either male or female)

test is currently available for the nest survival models in Mark program (Dinsmore et al. 2002; Cooch and White 2015).

Finally, Spearman's correlation analyses were conducted to assess the relationship between ranked behaviors and nest survival (i.e., days active).

RESULTS

Overall, we monitored 327 nests during this study (1993–2001; 2007–2008): 242 at Serradal beach, 29 at Almenara beach, and 56 at Punta beach. The main causes for clutch failure were predation (44.8%) and nest desertion (35.8%).

Nest defense

There was a positive correlation between female and male mean ranked behaviors within pairs (Spearman rank correlation: $r_s = 0.525$, $N = 225$, $P < 0.0001$; Figure 1). Nevertheless, there were differences in defensive behavior investment within the breeding pair. Mean ranked behavior (±SE) were 1.40 ± 1.10 and 1.85 ± 1.18 for males and females ($N = 225$ nests), respectively, and the difference between sexes was significant (Wilcoxon signed-ranks test: $Z = -6.693$, $N = 225$, $P < 0.001$), with females exhibiting riskier behavior.

The ground alarm calls behavior (i.e., ranked response 4) was seldom the riskiest recorded behavior exhibited by both sexes, and was frequently followed by mobile or stationary distractions (i.e., ranked responses 5 and 6, respectively). Nevertheless, the latter display (i.e., ranked response 6) was more often performed by females than males (11.61% of females and 0.89% of males) (Wilcoxon signed-ranks test: $Z = -5.548$, $N = 225$, $P < 0.001$).

Nest survival models

We created encounter histories for nest survival analysis in MARK for 225 nests, for which we recorded all covariates. We developed 49 candidate models in the 4-stage modeling procedure. The best model among multiple competing models resulting from the 3 first stages and all models created in the final stage are shown in Table 3.

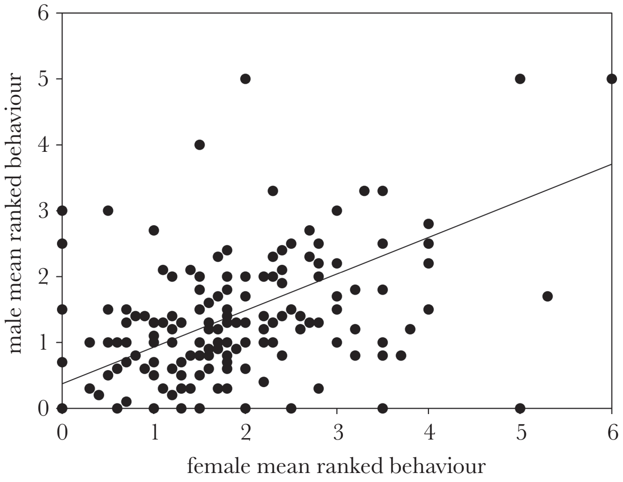

Figure 1

Relationship between nest defense intensity (mean ranked behavior) of male and female Kentish plovers within pairs ($N = 225$ nests).

Our modeling results produced 2 models with $\Delta AIC_c < 2$ in the final stage of model building, a single model with appreciable support ($\omega_i = 0.63$) and a second, less competitive model ($\omega_i = 0.28$). Both models jointly had a high support from the model set (summed $\omega_i = 0.90$; Table 3). The top-ranked models included 9 parameters and combined the additive effects of site, season (a quadratic trend time), habitat, and exposure. Both models were differentiated by the additive effects of behavioral parameters considered. The top-ranked model included the additive effect of the maximum value of female ranked behavior ($\beta = 0.52 \pm 0.11$, 95% CI = 0.32, 0.73; Table 4); the second model included the additive

Table 3

Selected models of Kentish plover nest survival analysis resulting from a 4-stage modeling procedure. The best model among multiple competing models resulting from the 3 first stages and all models created in the final stage are shown

Modeling stage	Model	AICc	Delta AICc	ω_i	Model likelihood	*K*	Deviance
4	{B0+T*T+Site+Habitat+ Exposure+ Max_ Female_behav}	320.09	0	0.63	1	9	302.05
4	{B0+T*T+Site+Habitat+ Exposure+%Female_behav}	321.74	1.65	0.28	0.43	9	303.70
4	{B0+T*T+Site+Habitat+ Exposure+ Female_behav}	324.12	4.03	0.08	0.13	9	306.08
4	{B0+T*T+Site+Habitat+ Exposure+ Max_ Nest_behav}	329.37	9.28	0.006	0.01	9	311.33
4	{B0+T*T+Site+Habitat+ Exposure+%Nest_behav}	330.35	10.25	0.004	0.006	9	312.32
4	{B0+T*T+Site+Habitat+ Exposure+ Total_nest_behav}	331.59	11.50	0.002	0.003	9	313.55
4	{B0+T*T+Site+Habitat+ Exposure+ Nest_behav}	332.44	12.35	0.001	0.002	9	314.40
4	{B0+T*T+Site+Habitat+ Exposure+ Max_ Male_behav}	341.60	21.51	0.00001	0	9	323.56
4	{B0+T*T+Site+Habitat+ Exposure+%Male_behav}	342.23	22.14	0.00001	0	9	324.19
4	{B0+T*T+Site+Habitat+ Exposure+ Male_behav}	345.07	24.98	0	0	9	327.03
3	{B0+T*T+Site+Habitat+ Exposure}	345.77	25.68	0	0	8	329.74
1	{B0+T*T+Site}	356.01	35.92	0	0	4	348.0
2	{B0+T*T+Site+Nest_age}	356.61	36.52	0	0	5	346.60
	{B0}	374.65	54.56	0	0	1	372.65

See variable description in Table 2. AICc, Akaike Information Criterion corrected for small sample size; *K*, number of parameters; ω_i, Akaike weights; T, time; T*T, quadratic time trend.

Table 4

Model estimates from Program MARK of covariates included in the top-ranked models of daily survival rate of Kentish plover nests. The covariates were considered biologically informative if their confidence intervals did not include 0

Parameter	B coefficient	SE	95% CI	
			Lower	Upper
Top-ranked model				
Intercept	0.024	0.993	−1.923	1.971
Quadratic time trend	**−0.000**	0.000	−0.000	−0.000
Site_Almenara	**−2.047**	0.590	−3.203	−0.891
Site_Serradal	0.177	0.454	−0.713	1.067
Habitat_ tidal debris	1.050	0.578	−0.083	2.183
Habitat_embryonic shifting dunes	**1.234**	0.536	0.184	2.283
Habitat_ shifting dunes	**2.043**	0.558	0.950	3.136
Exposure	**1.999**	0.531	0.958	3.040
Max_Female_behav	**0.522**	0.106	0.315	0.729
Second-ranked model				
Intercept	1.628	0.986	−0.304	3.560
Quadratic time trend	**−0.000**	−0.000	−0.000	−0.000
Site_Almenara	**−2.289**	0.608	−3.480	−1.097
Site_Serradal	−0.103	0.457	−0.998	0.793
Habitat_tidal debris	0.930	0.605	−0.256	2.117
Habitat_embryonic shifting dunes	**1.118**	0.551	0.038	2.198
Habitat_shifting dunes	**1.960**	0.548	0.886	3.034
Exposure	**1.715**	0.537	0.662	2.767
%Female_behav	**0.036**	0.008	0.019	0.053

Bold text denotes B coefficients with 95% CIs that did not overlap zero. See variable description in Table 2.

effect of the percentage of female ranked behavior values higher than 2 (β = 0.04 ± 0.01, 95% CI = 0.02, 0.05; Table 4).

DSR decreased as the breeding season progressed. Thus, nests that started later in the season had a lower survival probability (Figure 2). In the best model, we found a strong positive relationship between DSR and the *maximum value of female ranked behavior* (Table 4). Therefore, nests defended by females with riskier distraction behaviors had greater DSR (Figure 3). We also found a strong positive relationship between DSR and the *embryonic shifting dunes* and *shifting dunes* habitats. Tidal debris habitat had a weak positive relationship with DSR; the 95% CI of the estimate overlapped 0. Finally, we also found a strong positive relationship between DSR and *exposure*, with greater DSR for nests on unexposed nest sites.

Covariates used to estimate the effect of the *Year*, *Management*, *Seashore*, *Nest_age*, and *Nest_season* (see variable description in Table 2) were not included in any of the top-ranked models. In the second ranked model, we found a weak positive relationship between DSR and the *percentage of female ranked behavior values higher than 2*, which meant that nests defended by females who assumed more predation risk throughout the incubation period had greater DSR (Figure 3).

DISCUSSION

Our results show that Kentish plover's nests in which parents invested more on defense survived longer, thus suggesting that defensive behaviors must play a critical role in nest survival. Interestingly, we found differences in nest defense investment among members of breeding pairs, with females performing riskier defensive behaviors than males. In this respect, stationary distractions were performed by females in almost 12% of the nests, but less than 1% by males.

Kentish plover females generally incubate during daytime (Fraga and Amat 1996), although males also cooperate in situations of heat stress (Amat and Masero 2004a; Alrashidi et al. 2010). In our study, all experiences of nest approaching were performed during daytime. Consequently, the lower response of males found in this study might be accounted for by their absence from nests at the time our experiments were carried out. Nevertheless, males and females were present (i.e., ranked response > 0) in 87.6% and 92.0% of the nests approaches, respectively. Furthermore, both sexes often displayed defensive behavior, since there was some type of distraction display (average percentage of ranked response > 2) in 55.1% and 69.8% of nests for males and females, respectively. Sex differences in defense investment are common in birds, and females normally perform more intense defensive behaviors, in accordance with their greater reproductive investment (Montgomerie and Weatherhead 1988; Møller and Nielsen 2014). Nevertheless, the contribution of both sexes to nest defense in shorebirds should have a direct link with nest survival, although this relationship has only been demonstrated for species with biparental incubation (Smith and Wilson 2010).

Predator approaching and distraction displays are part of the Kentish plover's tactics to assess risk and minimize predation. Birds inform their mate or chicks of potential threats by emitting alarm calls or signals (Simmons 1955b). Under a more obvious potential threat, parents may adopt other antipredator tactics, such as distraction displays (Gochfeld 1984). Our results showed that in 87.1% of nests at least 1 member of the pair approached the observer and remained vigilant, performing some type of active distraction displays in 74.2% of the studied cases (i.e., ranked response >2). In this respect, both sexes emitted ground alarm calls initially, and very often this was followed by riskier behaviors, such as mobile or stationary distraction displays.

Investment in antipredator defense should be proportional to predation risk (Lima and Dill 1990), but the effectiveness of distraction displays is probably linked to the risk assumed (Sordahl 1990b; Caro 2005). Similar to our findings, Byrkjedal (1987) showed that Eurasian dotterel, *Charadrius morinellus*, nests in which parents performed stationary distraction displays had greater success than those in which parents performed mobile displays only. Although the benefits of offspring defense are beyond question, defensive behavior increases the probability of death or injury of adults, and moreover reduces the available time for other reproductive duties (Walters 1982; Montgomerie and Weatherhead 1988; Møller and Nielsen 2014). Notwithstanding, fatal outcomes for birds performing distraction behaviors are expected to be rare, since high risk behaviors would otherwise not be selected if the chances of a fatal outcome outweighed benefits (Gochfeld 1984). In fact, only a few studies have documented cases of birds being preyed upon while performing distraction behaviors (Sordahl 1990a; Brunton 1986). Nevertheless, although these predation events should be rare, their importance should not be neglected (Brunton 1986; Lima and Dill 1990; Sordahl 1990a; Lima 1993). Amat and Masero (2004a) described 2 cases of Kentish plovers that were preyed upon while performing displays, one of them by a kestrel and the other by dog. In our study area, we observed only one case of predation by a kestrel while plovers were performing displays. Furthermore, domestic dogs were usually walked along the studied beaches and frequently chased plovers, and this resulted in some nest failures (Gómez-Serrano and López-López 2014). Indeed, we frequently observed dogs attempting to capture plovers during distraction displays and we surmise that predation by these animals could be significant.

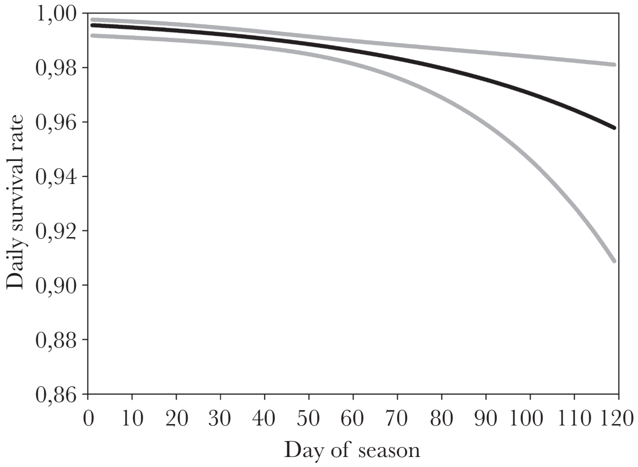

Figure 2
Relationship between NS date and DSRs (black line) with 95% confidence intervals (grey lines) of Kentish plover nests in the study area. Day 1 corresponds to 14th March.

Plovers avoid nesting in vegetated areas so as to increase predator detection (Page et al. 1985; Warriner et al. 1986; Martin 1988; Fraga and Amat 1996; Amat and Masero 2004a; Muir and Colwell 2010; Saalfeld et al. 2011; Anteau et al. 2012a; Gómez-Serrano and López-López 2014). Hence, it is expected that birds nesting in exposed sites will exhibit more intense defensive behaviors in order to compensate for the greater detectability of their nests by predators (Larsen et al. 1996). On the other hand, Amat and Masero (2004a) showed that females nesting in unexposed sites had a lower body condition, presumably because they were unable to cope with the heat stress of exposed locations. We found that *exposure* was a habitat covariate retained in the top-ranked nest survival models, showing a strong positive relationship with DSR. Nests located in unexposed sites had greater DSR. Nevertheless, contrary to our expectations, males and females nesting in unexposed sites invested twice as much in nest defense (mean % ranked response > 2; males: unexposed 31.2%, exposed 18.2%, Mann–Whitney U test: $U = 4502.5$, $N = 225$, $P = 0.00056$; females: unexposed 39.4%, exposed 25.4%, Mann–Whitney U test, $U = 4654.0$, $N = 225$, $P = 0.00254$) as compared to those nesting in exposed sites. This apparent contradiction can be accounted for by environmental differences among both habitat types. Unlike the population studied by Amat and Masero (2004a), which bred in an inland saline lake, plovers in our study area bred on sandy beaches, where exposed nests were placed in vegetation-free areas, in the area comprised between shifting dunes and the seashore. These sites are exposed to the sea breeze, which

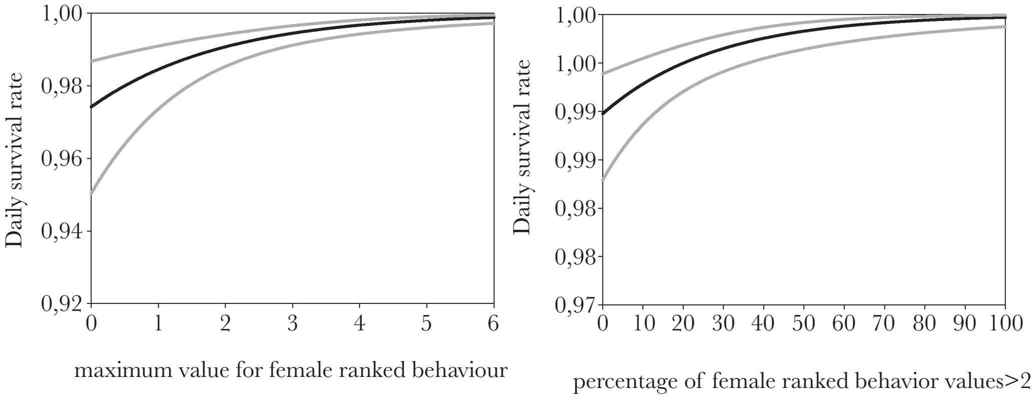

Figure 3
Daily survival rates (black line) with 95% confidence intervals (grey lines) of Kentish plover nests in relation to female investment in defense behavior: maximum recorded value of ranked behavior (left) and percentage of active distraction displays (right).

may have a thermoregulatory effect that alleviates heat stress on eggs and the incubating adult (authors' unpublished data). Thus, nests in unexposed sites might experience higher temperatures and therefore be more vulnerable to egg or embryo loss during prolonged absence of incubating adults. This might explain why birds nesting in unexposed sites in our area performed more intense and risky distraction displays in order to move the predator away as soon as possible, thus avoiding egg loss to overheating.

Distraction behavior has been shown to vary depending on predator type (e.g., terrestrial, aerial, mammal, etc.) (Byrkjedal 1987; Brunton 1990; Caro 2005; Šálek and Cepáková 2006), predator proximity (Sordahl 1986; Byrkjedal 1989), or the degree of risk assumed by the bird while defending its offspring (Montgomerie and Weatherhead 1988; Brunton 1990). For instance, distraction behavior is often displayed against ground predators, particularly mammals, but seldom against avian predators (Armstrong 1954; Byrkjedal 1989; Sordahl 1990b). Obviously, the bird assumes this risk posed by this conduct because it ultimately contributes to increase its fitness. Consequently, the intensity of distraction behaviors should be linked to the ability of the predator to pinpoint its nest. In this respect, human presence was likely to elicit defensive behaviors similar to those triggered by other terrestrial predators, since animals have developed antipredator responses to generalized threatening stimuli (Frid and Dill 2002; Graham et al. 2005). Indeed, humans are commonly used in studies dealing with offspring defensive behavior (Byrkjedal 1987, 1989; Brunton 1990; Sordahl 1990b; Pavel et al. 2000; Lord et al. 2001; Brown and Brown 2004; Yasué and Dearden 2006; Møller and Nielsen 2014). In a previous study, we found that birds modulate flushing behavior depending on both predator type (i.e., higher response against people walking with unleashed dogs than against people without dogs) and the intensity of human disturbance, and that birds habituated to human presence tolerate closer approaches (Gómez-Serrano and López-López 2014). Nevertheless, the selected models did not include human disturbance. Indeed, there were no significant differences in the defensive behavior of females and males among disturbed and undisturbed beaches (mean ranked response; males: undisturbed 1.2, disturbed 1.5, Mann–Whitney U test, $U = 4207.0$, $N = 225$, $P = 0.3243$; females: undisturbed 2.0, disturbed 1.8, Mann–Whitney U test, $U = 3866.0$, $N = 225$, $P = 0.071$). This suggests that plovers consider humans as potential predators (Roberts and Evans 1993; Schulz and Stock 1993; Webber et al. 2013) and, consequently, their presence triggers antipredator responses of incubating birds.

We found that the substrate on which nests were placed was not retained in the top-ranked nest survival models. This contrasts with other studies on nest-site selection by plovers, in which substrate type was linked to nest survival (Colwell et al. 2011; Anteau et al. 2012b; Skrade and Dinsmore 2013). We hypothesize that the lack of relationship between substrate and nest survival may be explained by the simplistic nature of the variable used. Indeed, nest location was defined using a binary variable, which allowed us to differentiate between nests on sand or pebbles. Nevertheless, even though egg crypsis may differ between both substrates, other underlying factors could affect nest detectability by predators, such as egg color, background matching (Lovell et al. 2013; Skrade and Dinsmore 2013), substrate heterogeneity, or frequency of egg-sized stones (Colwell et al. 2011).

Individual behavioral differences may increase adult and offspring survival (Smith and Blumstein 2008). The behavior of incubating birds may increase breeding success through reducing predation risk of both adults and offspring. In this line, arctic shorebirds taking fewer incubation recesses showed higher nest success, presumably as a result of a lower detectability by predators (Smith et al. 2007, Smith et al. 2012). Other studies reveal that flushing behavior of incubating shorebirds influenced nest survival (Koivula and Rönkä 1998; Amat and Masero 2004a; Gómez-Serrano and López-López 2014). Despite the importance that defensive behaviors of incubating adults may have on breeding success, few studies have explored this relationship (Byrkjedal 1987; Smith and Wilson 2010) and practically none have incorporated them as covariates in nest survival models (Colwell et al. 2011). This situation is paradoxical, given the abundance of studies on defensive behavior and short-term changes in predation risk (Frid and Dill 2002).

In conclusion, our study highlights that increased risk assumption in offspring defense by adults is advantageous in terms of individual fitness, providing further insight into the relative contribution of distraction displays on nest survival. On the other hand, the greater investment in nest defense by females with regard to males revealed by our experiments could be tentatively explained by greater investment in reproduction in the case of females.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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