



Male but not female Kentish plovers *Charadrius alexandrinus* modulate foraging behaviour according to tide during incubation

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Abstract

During breeding, birds have to find a balance between reproductive tasks and the need to recover their energy. Foraging movements are constrained in time and space by brood guarding and chick-rearing activities at the nesting site. Foraging behaviour differs among species according to their ecology but it can change, even markedly, among individuals of the same species according to intrinsic and extrinsic factors, such as sex, habitat, intra and inter-specific interactions. By means of individual GPS tracking, we assessed foraging behaviour of egg-incubating Kentish plovers breeding along a sandy beach bordering the Venice Lagoon. Both sexes foraged on the beach where they bred, but also in the lagoon, travelling up to 16 km far from the nest. In both habitats, individuals foraged in areas that were significantly separated from those used by other tagged conspecifics, likely lowering intra-specific competition. Males foraged mainly at daytime, in the lagoon at low tide and on the beach at high tide. Differently, females foraged mainly at night and in the lagoon, and less often on the beach exclusively during daytime, regardless of tide height. The avoidance of nocturnal foraging on the beach by females might be explained as antipredatory response to the presence of owls breeding in a pinewood adjacent the beach or to a possible diet specialization on prey that are available in the lagoon at night, irrespective to tide conditions. Overall, this study revealed an unexpected sexual difference in foraging behaviour of Kentish plover, with sexes likely facing different environmental pressures according to diurnal and nocturnal foraging.

Keywords Breeding · GPS tracking · Movement ecology · Sexual dimorphism · Predation

Zusammenfassung

Männliche, aber nicht weibliche Seeregenpfeifer (*Charadrius alexandrinus*) steuern während der Brutzeit ihre Nahrungssuche in Abhängigkeit von den Gezeiten

Während des Brütens müssen Vögel ein ausgewogenes Verhältnis zwischen der Brutpflege und der Notwendigkeit, wieder Energie aufzutanken, finden. Die Futtersuche wird in der Tat durch die Brutpflege und die Aufzucht der Küken im und am Nest

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zeitlich und räumlich eingeschränkt. Das Verhalten bei der Futtersuche hängt von den jeweiligen Umgebungsbedingungen ab und unterscheidet sich zwischen den einzelnen Arten, kann aber auch zwischen Einzeltieren derselben Art unterschiedlich sein, sogar sehr, je nach inneren und äußeren Faktoren wie Geschlecht, Lebensraum und inter- und intraspezifischen Interaktionen. Anhand von GPS-Ortung haben wir das Futtersuchverhalten von an einem Sandstrand am Rande der Lagune von Venedig brütenden Seeregenpfeifern nach der Eiablage untersucht. Beide Geschlechter suchten an dem Strand, an dem sie brüteten, nach Nahrung, aber auch in der Lagune, in der sie sich bis zu 16 km von ihrem Nest entfernten. In beiden Lebensräumen gab es einzelne Tiere, die in Arealen nach Nahrung suchten, die deutlich von denen getrennt waren, in denen andere markierte Artgenossen unterwegs waren; vermutlich verringerten sie so die innerartliche Konkurrenz. Die Männchen suchten vorwiegend tagsüber nach Nahrung, bei Ebbe in der Lagune und bei Flut am Strand. Im Gegensatz dazu waren die Weibchen vorwiegend bei Nacht in der Lagune unterwegs, am Strand hingegen weniger oft und ausschließlich tagsüber, unabhängig von der Höhe der Flut. Das Vermeiden der nächtlichen Nahrungssuche der Weibchen am Strand könnte als Räubervermeidungs-Strategie in Hinblick auf Eulen erklärt werden, die in einem angrenzenden Kieferwald brüteten oder auch als Nahrungs-Spezialisierung auf Beutetiere, die nachts unabhängig von den Gezeiten in der Lagune verfügbar sind. Insgesamt zeigte die Untersuchung einen unerwarteten Geschlechtsunterschied im Futtersuchverhalten von Seeregenpfeifern, wobei Männchen und Weibchen vermutlich je nach Tages- und Nachtsuche unterschiedlichen Umgebungsanforderungen ausgesetzt waren.

Introduction

During reproduction, birds must optimize the time devoted to foraging according to brood guarding and chick-rearing activities. To comply successfully with such breeding duties, breeders need to rely on food resources located in areas reachable from the nest site in a time that do not compromise nest attendance and offspring needs. Foraging behaviour of breeding birds may vary widely among species according to their ecology and characteristics. For instance, tube-nose species may cover large distances during foraging trips thanks to their ability of exploiting winds over the sea surface and the particular physiology of chicks that allow them to be fed no more than once a day; the large Black-browed Albatross *Thalassarche melanophrys* and the small European Storm Petrel *Hydrobates pelagicus* can travel up to 8000 and 1000 km respectively during a single foraging trip undertaken during egg incubation (Philips et al. 2004; De Pascalis et al. 2021). However, most of the land bird species forage within few kilometres from the nesting site; e.g. 1–7 km in shorebirds (Schwemmer and Garthe 2011; Caccamo et al. 2011; De Marchi et al. 2015), ca. 3 km in European Nightjar *Caprimulgus europaeus* (Evens et al. 2018) and 6 km in the Lesser Kestrel *Falco naumanni* (Cecere et al. 2020). Within species, the extension of foraging movements of individual breeders may vary according to both external and internal factors, such as the quality of habitats surrounding the breeding site (Cecere et al. 2014), the individual experience and/or age (Catry et al. 2006, 2011) and personality (Patrick et al. 2017). In some cases, individuals may consistently use specific foraging locations that are separated from those used by conspecifics. The individual foraging site fidelity can lower intra-specific competition during the entire breeding period (Wakefield et al. 2015) or during a specific stage, such as during chick-rearing in Lesser

Kestrels (Ramellini et al. 2022). Spatio-temporal characteristics of foraging behaviour may also differ between sexes, generally due to different parental roles or to sexual differences in body size and morphology. For instance, chick-rearing female Scopoli's Shearwaters *Calonectris diomedea* generally forage farther than males under low wind conditions, thanks to their lower wing loading that allow them to exploit wind conditions more efficiently (De Pascalis et al. 2020). Another example is the one of Andean Condor *Vultur gryphus*, where males schedule foraging trips earlier in the morning, aligning their flights to the most profitable uplift conditions compared to females that are smaller, resulting in temporal partitioning between sexes (Alarcón et al. 2017).

In some bird species, foraging behaviour is shaped also by moon cycle, directly (i.e. Rubolini et al. 2015) or indirectly. The latter is the case of wader birds, which feed on invertebrates mainly in intertidal areas, where prey become more available during low-tide (Rosa et al. 2007). As a result, timing of foraging activity of waders tends to match tidal cycle (Van de Kam et al. 2004; Granadeiro et al. 2006).

With this study, we aimed to describe for the first time to our knowledge the foraging behaviour of breeding Kentish Plovers *Charadrius alexandrinus*, a small wader with sexual plumage dimorphism, by means of GPS-tracking. Compared to observation-based studies (e.g. Castro et al. 2009), GPS-tracking data are not biased by positions of observers and provide information about the behaviour of target individuals also during nighttime, which might be crucial to describe movement patterns of female Kentish Plovers. Indeed, in this wader bird, both parents are involved in the incubation of eggs, with females attending the nest mainly during daytime and foraging at night, while males do the opposite (Nazakawa 1979; Fraga and Amat 1996). We expected that such temporal segregation in foraging activity might produce sex-based differences in foraging behaviour. We hence investigated whether the habitat

exploited for foraging and the distance of foraging areas from the nesting site differed between the sexes during incubation. In addition, we assessed whether individual foraging site fidelity occurs in breeding Kentish Plovers, as observed in other shorebird species (Schwemmer and Garthe 2011). Finally, we assessed the effect of tide on foraging behaviour of males and females. During breeding, birds have a high energetic demand and waders might need to find food also when the tide is high. In the study area, Kentish plovers can rely on both the sandy beach and the Venice Lagoon for feeding. We expected that the decision to forage in one of the two habitats depends on tidal conditions, with the lagoon that is well characterised by tidally structured environments being more exploited when tide is low, while the beach in high tidal conditions. In this case, we did not expect any sexual difference in the behavioural response to tide, since both sexes can experience low and high tide despite the daily temporal segregation in foraging.

Materials and methods

Study area and target species

The study was conducted along the coast of Cavallino-Treporti (45°26'34''N 12°27'42'' E), a 13 km-long beach that borders the Venice Lagoon (Italy), where on average 24–29 individuals of Kentish plover breed every year, resulting on average in 20 nests with eggs, including unsuccessful ones, per year (2017–2019 own data). The Kentish Plover is a small (mean \pm SD body mass: 45.3 \pm 2.9 g; data from studied population, $N=18$, min–max: 40.0–50.0 g) sexually plumage dimorphic shorebird species, with males, but not females, exhibiting neat black markings on head and breast sides, and rusty crown and nape. It is a ground-nesting bird, breeding mainly close to wet habitats, such as beaches, marshes, shore of saline lakes, lagoons and coasts, but also in alkaline grasslands and semi-arid desert (Colwell and Haig 2019). The female generally lays three eggs (rarely 2 or 4) that are incubated for ca. 28 days by both sexes.

GPS deployment

We trapped 20 individuals sitting on eggs using a drop trap placed on the nest after the tenth day from the laying of the last egg, between mid-April and early-June 2018 and 2019. Upon capture, we ringed birds with both metallic and darvic colour alphanumeric rings, recorded the sex and measured the body mass using a spring balance (± 0.1 g). We then deployed a GPS logger (1 g PinPoint-10 by Lotek UK Ltd) using a leg loop made of silicon ring. Birds were eventually recaptured using the same method of the first capture after ca. 5 days from tagging. The total mass of the deployed devices (including leg loop) was 1.2 g, which never exceeded the 3% of bird

body mass (range: 2.4–3.0%). GPS loggers were set to record locations at 2 h intervals during both day and nighttime.

We recaptured 18 out of 20 GPS-tagged birds, but three of them were not included in the study for the following reasons: (1) the logger of one bird stored no data; (2) one bird lost the logger; (3) one, together with its partner, abandoned the nest two days after logger deployment and it was recaptured during the second breeding attempt but most of GPS data was recorded when the bird was not breeding. Ultimately, we relied on 15 breeders (7 males and 8 females) tracked for 4.4 ± 1.5 (SD) days (range 1.2–6.1) during incubation, for a total of 797 GPS locations (see Fig. 1).

Ethical note

Capture, handling and tagging procedures were conducted by the Italian Institute for Environmental Protection and Research (ISPRA), under the authorization of Law 157/1992

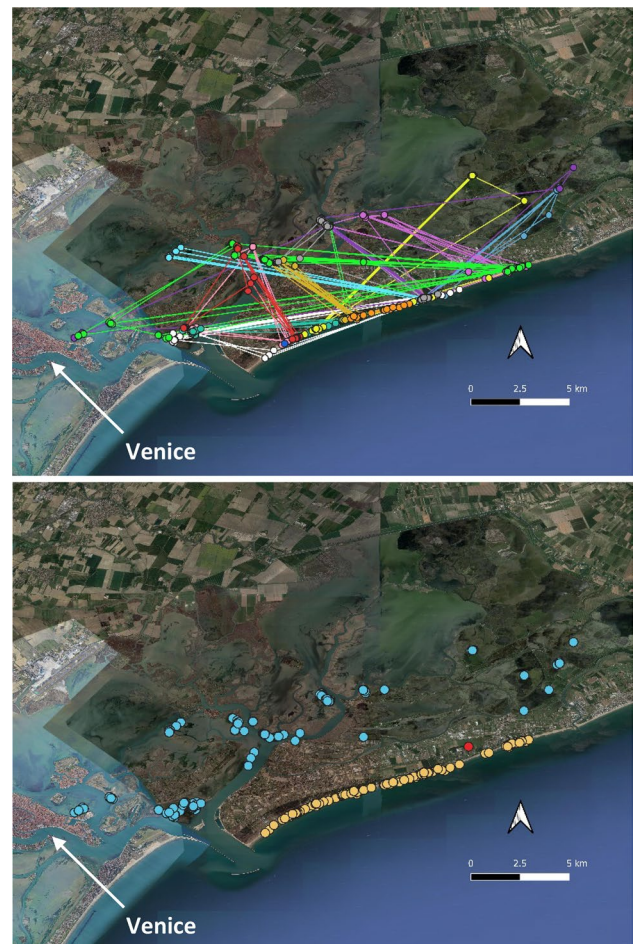


Fig. 1 Foraging trips performed by 15 Kentish Plovers (each represented by a different colour) during the egg incubation stage (upper panel), and GPS positions classified according to habitat type (lower panel); lagoon (light blue), beach (dull yellow) and urban areas (red). The arrow points to the city of Venice

[Art.4(1) and Art7(5)], which regulates research on wild bird species. Birds were handled by experienced staff only and no bird was injured by the capture/handling procedure. Handling lasted less than 10 min, after which the bird was released close to its nest. To minimise any possible detrimental effect on the breeding, we tagged only one member of the pair. After tagging and second handling, all birds returned to the nest for incubating (checked with a spotting scope), with the exception of one bird that did not return to the nest, but it was regularly observed around the study area for the entire breeding season. The proportion of abandoned clutches for nests where one of the breeders was tagged (0.4) was in line with (and actually lower than) the one of control nests (0.7) during the two study years. However, it should be noted that control nests included also replacement clutches, which generally have a lower hatching success. Overall, these results suggest a negligible effect of tagging on breeding performance, at least for the short tracking period (ca. 5 days). No predation occurred during incubation because all nests in study area were covered with a cylindrical cage allowing Kentish Plovers to move through the mesh but preventing egg predations by medium-sized mammals (foxes, cats and dogs) and birds (gulls and crows).

Egg incubation and foraging activity

During the egg incubation stage, Kentish Plovers alternate breeding and foraging duties. To associate each GPS position to one of the two activities (incubation/foraging), we first measured for each individual the distance of all GPS locations from the nest by means of the function *distance* of the “argosfilter” R package (Freitas 2012). After inspection of the distribution of distances of GPS locations from the nest (see Supplementary Figure S1), and supported by direct observations, we attributed to incubation all GPS locations being ≤ 25 m distant from the nest, and to foraging (and to a lesser extent, relocation) those being > 50 m distant from the nest. The threshold of 25 m for incubation considers also short movements (e.g., when the incubating parent walks away briefly after being disturbed) during incubation activity. GPS locations between 25 and 50 m were of uncertain classification and were thus not included in the analyses. Finally, we discarded seven implausible GPS positions out of 804 after visual inspection (i.e. unreliable distances covered in the time between two points, which is 2 h).

To assess sexual differences in the timing of incubation, we fitted a binomial Generalized Linear Mixed Model (GLMM) with the type of activity (incubation/foraging) as binomial response variable, sex and daytime (day/night) and their interaction as fixed factors, and bird identity as random intercept. Daytime was identified by comparing local time (hh:mm) associated to each GPS location to the civil twilight (dawn and dusk) obtained by means of the function

getSunlightTimes of the “suncalc” R package (Thieurmel and Elmarhraoui 2019).

Effect of tide on foraging habitat type

All foraging locations were associated with the habitat where they occurred using the Corine Land Cover map 2018. For the purpose of this study, the classes “beaches/dunes” and “sea” (corresponding to foreshore locations) were merged in the “beach” habitat type, while classes “coastal lagoon” and “salt marshes” were merged to create the “lagoon” habitat type.

To assess possible sexual differences in the distance of foraging areas from the nest, we fitted a GLMM (using a log link function) with the distance of foraging locations from the nest as dependent variable, sex (female and male), habitat type (beach and lagoon, i.e. the two habitats used for foraging; see Results), sampling year (2018/2019) and the interaction between sex and habitat type as fixed factors; bird identity was entered as random intercept. To assess whether tidal conditions affected the decision to foraging on the beach or in the lagoon, we fitted a binary GLMM with habitat type associated to each foraging location (beach/lagoon) as response variable, tide height, sex and daytime (day/night) as fixed factors, and bird identity as random intercept. We also tested the two-way interactions of sex with tide height and with daytime. Tide height was obtained from the Meteomareographic network of the Venice Lagoon (<https://www.venezia.isprambiente.it/meteo-mareographic-network>): among the 26 active tide gauge stations we selected the two ones, namely Sant’Erasmus and Grassabò, which were close to the study area and for which a complete time series of data (at 10 min interval) was available for the whole study period. We then averaged the values of the two stations and attributed to each foraging location the tide value nearest in time. For both the analyses previously described we considered only locations > 50 m far from the nest, to exclude leaving or approaching movements to the nest during foraging activity.

Individual foraging site fidelity

To assess whether individuals used foraging areas that are distinctly separated from those used by other tagged conspecifics when foraging on the beach or in the lagoon, we calculated for each individual and habitat the median location of all foraging locations occurring within each day/night interval (i.e. each daytime and each nighttime) during which each bird was tracked. We considered such median location as representative of the foraging area exploited by a tagged bird during each day or night of the tracking period. Intervals with less than 3 foraging locations were discarded. Following Votier et al. (2017) and Sztukowski et al. (2018), we then assessed individual foraging site fidelity by estimating

Table 1 Outputs of the regression models fitted to assess the effect of the reported predictors on 1. the probability to perform incubation vs foraging activity (binary GLMM), 2. the distance from the nest of

foraging locations (GLMM with log link), 3. the probability to forage in the lagoon vs beach (binary GLMM)

Predictors	Estimate ± SE	X ²	df	P
1. Activity (0 = foraging, 1 = incubation): N = 797				
Intercept	- 2.01 ± 0.34	-	-	-
Sex	2.93 ± 0.45	22.71	1	< 0.0001
Day/night	2.79 ± 0.29	42.41	1	< 0.0001
Day/night*sex	- 8.12 ± 0.80	102.24	1	< 0.0001
2. Distance of foraging locations from the nest: N = 468				
Intercept	- 0.71 ± 0.24	-	-	-
Sex	0.64 ± 0.31	0.03	1	0.86
Habitat type	2.69 ± 0.21	319.26	1	< 0.0001
Sampling year	- 0.07 ± 0.20	0.12	1	0.72
Habitat type*sex	- 0.72 ± 0.26	7.93	1	< 0.01
3. Foraging habitat type (0 = beach, 1 = lagoon): N = 468				
Intercept	0.90 ± 0.90	-	-	-
Tide hight	- 0.03 ± 0.01	11.39	1	< 0.001
Sex	- 5.57 ± 1.73	0.12	1	0.73
Day/night	0.22 ± 0.44	1.81	1	0.18
Tide hight*sex	0.04 ± 0.02	4.43	1	0.04
Day/Night*Sex	6.79 ± 1.64	17.07	1	< 0.0001

Individual identity (N=15) was entered as a random intercept effect in all models. Sex was coded as 1=males and 2=females; Day/Night as 1=day and 2=night. Models were not overdispersed ($\Phi < 1$). Degrees of freedom for F tests were estimated with a Kenward-Roger (type III) test

P-values lower than 0.05 are in bold

the repeatability of either latitude or longitude of the median location using the “rptR” R package (Stoffel et al. 2017), including individual identity as random intercept (i.e. unadjusted repeatability), separately for beach and lagoon habitat

and for the two sampling years. Significance of repeatability estimates was tested through permutation of residuals (1000 permutations) and 95% confidence intervals (CI) by parametric bootstrapping (1000 bootstraps) (Stoffel et al. 2017).

Fig. 2 Predicted probability of incubation vs. foraging activity according to day/night for males and females, with corresponding 95% confidence intervals (light colour bands), as estimated by the binomial GLMM reported in Table 1 (model n.1). Rugs along horizontal axes represent the position of observations. Plots generated in R using the package visreg (2.6.0) (Breheny and Burchett 2017). Kentish plover pictures from a modified photo by M. Basso

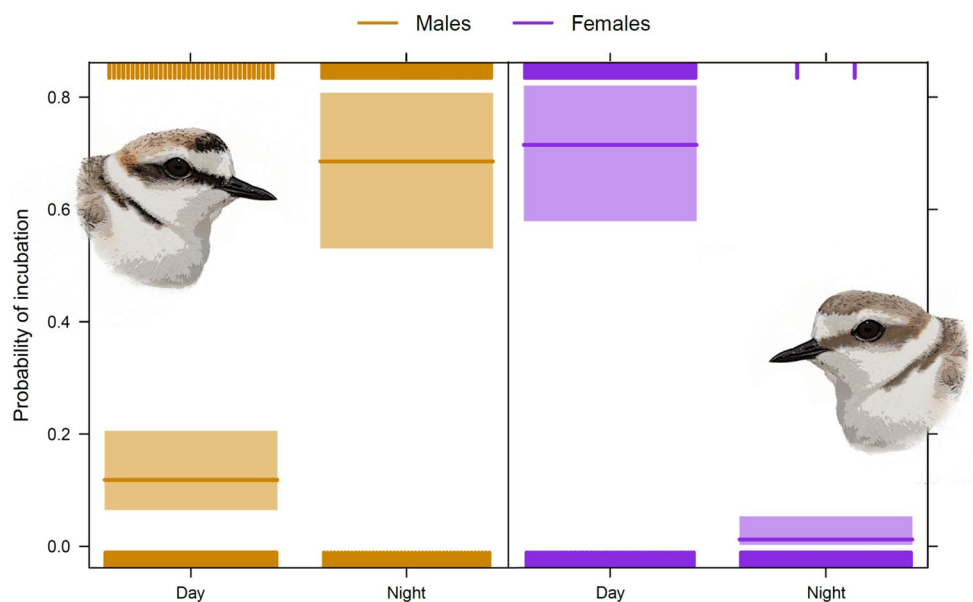
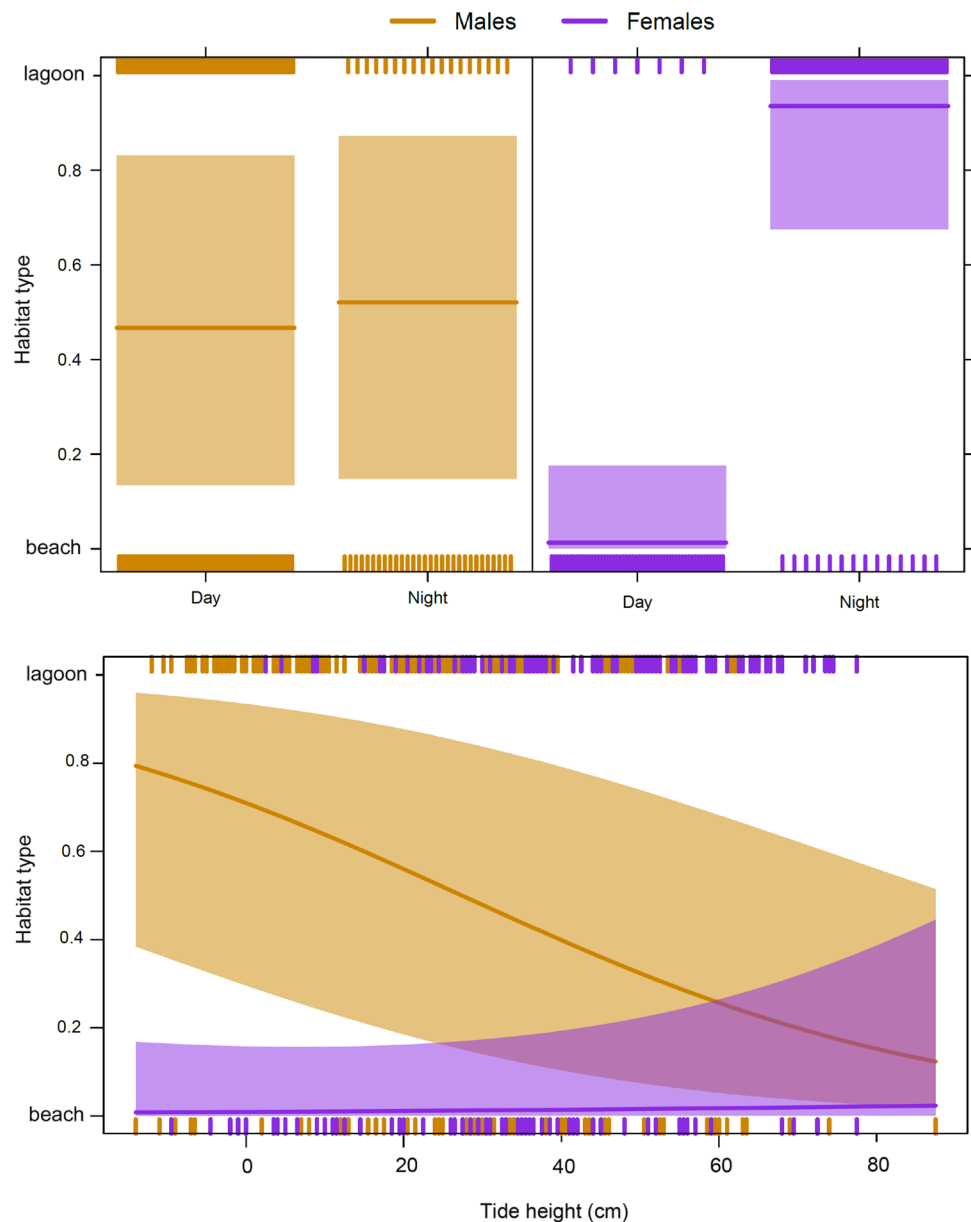


Fig. 3 Predicted probability of foraging in lagoon vs. beach according to day/night (upper panel) and tidal condition (lower panel) for males and females with corresponding 95% confidence intervals (light colour bands), as estimated by the binomial GLMM reported in Table 1 (model n.3). Rugs along horizontal axes represent the position of observations. Plots are conditional on all components of the predictor, i.e. they show the change in response on the y-axis, holding all other variables constant (upper panel: median of tide height; lower panel: most common category of factor day/night – “day” in this case)



Following Potier et al. (2015), we considered repeatability estimates high if $R > 0.5$, moderate if $0.25 \leq R \leq 0.50$ and low if $R < 0.25$.

Results

The probability of being in incubation vs foraging was higher during the night for males, and during the day for females (Table 1 and Fig. 2). Foraging occurred in two different habitats: the beach where birds were nesting, accounting for 38.2% of foraging locations, and the lagoon (61.8%) (Fig. 1). Only one location was recorded on non-irrigated arable land, likely on a passage between the two previously described habitats. The distance from the nest of the foraging

Table 2 Unadjusted repeatability estimates of latitude and longitude of the median foraging location in the beach and in the lagoon, separately for the two sampling years, estimated from intercept-only linear mixed models

Median foraging location	2018		2019	
	$R_{\text{perm}} \pm SE$	P_{perm}	$R_{\text{perm}} \pm SE$	P_{perm}
Beach (Lat)	0.57 ± 0.22	0.007	0.95 ± 0.93	0.002
Beach (Lon)	0.62 ± 0.22	0.005	0.94 ± 0.11	0.001
Lagoon (Lat)	0.97 ± 0.44	0.001	0.73 ± 0.19	0.001
Lagoon (Lon)	0.97 ± 0.43	0.001	0.93 ± 0.86	0.001

locations on the beach was on average 0.69 km (median 0.16 km; Q1–Q3 0.10–0.47 km; max 7.81 km), while foraging areas in the Venice Lagoon were further away from the nest than those on the beach, on average 7.32 km (median: 5.46 km; Q1–Q3 4.97–9.13 km; max: 15.79 km). Males foraged on average closer to the nest than females when on the beach, while no sex-specific difference was detected when birds foraged in the lagoon (Table 1; see also Supplementary Figure S2).

Tide affected foraging behaviour of males that showed a higher probability of foraging in the lagoon during low tide and on the beach during high tide (Table 1 and Fig. 3). However, tide did not affect foraging behaviour of females, which foraged exclusively in the lagoon at night and on the beach in the daytime (Table 1 and Fig. 3). Individual foraging site fidelity was high in both the lagoon and the beach, with individuals consistently exploiting spatially distinct foraging areas during both sampling years (Table 2; see also Supplementary Figure S3).

Discussion

Using GPS-tracking, we investigated the foraging behaviour of incubating Kentish Plovers breeding along the beach bordering the Venice Lagoon. We found that incubating birds foraged in two different habitats, namely the beach where they breed and the lagoon. To reach foraging areas in the lagoon, they travelled up to 16 km far from the nest, flying over the urbanized area bordering the nesting site. When on the beach, males generally foraged closer to the nest than females, while no sexual difference was detected in the lagoon. Males foraged mostly during the day, in the lagoon during low tide and on the beach when tide was high. Differently, females foraged in the two habitats irrespectively of tide, but in the lagoon only at night and on the beach exclusively during the daytime. Overall, individuals used foraging areas that were separated from those used by the other tagged conspecifics, both on the beach and in the lagoon.

In accordance with previous studies (e.g. Nakazawa 1979; Fraga and Amat 1996), we found that Kentish Plover males mainly incubated at night and foraged during daytime, while females did the opposite. However, we also found that males occasionally incubated (or stayed in the proximity of the nest) also during the day, while females never incubated during the night. One possible explanation, supported by direct observations, is that the higher disturbance occurring during the day (i.e. from crows, gulls, humans and dogs passage) led the non-incubating (male) parent to guard the nest area from time to time, ready to take the place of the female when she flees because disturbed.

The exploitation of two different foraging habitats implied marked differences in movement behaviours. When on the

beach, birds exploited areas more or less close to nest (average 0.7 km far from the nest), with males foraging on average closer to the nest than females likely to guard the nest in case of any disturbance to the incubating female. When targeting the lagoon, males and females performed wide-ranging movements (average 7 km), greater than expected if compared to those of even larger shorebirds (e.g. ca. 1 km in the Eurasian Oystercatchers *Haematopus ostralegus*, Schwemmer and Garthe 2011; 3 km in the Stone-curlew *Burhinus oedicnemus*, Caccamo et al. 2011; 7 km in Crab Plover *Dromas ardeola*, De Marchi et al. 2015). The long incubation shifts of the species likely allow birds to forage far and reach profitable areas while the partner is on the eggs.

As expected (e.g. Castro et al. 2009), Kentish Plover males foraged in the two different habitats according to tidal conditions. They foraged in the lagoon when the tide was low, benefitting from the emergence of intertidal areas that makes small invertebrates more available to small waders. When the tide is high, such habitats are no longer available, and males foraged on the beach that is wide enough to allow birds to forage also in such conditions (Burger et al. 1997). Surprisingly, females did not modulate their foraging behaviour in relation to the tide. Indeed, they foraged exclusively in the lagoon during night and on the beach during daytime, irrespectively of tidal conditions. While the latter behaviour is likely due to the need of staying around the nest during the day (i.e. when female are expected to incubate), the avoidance of nighttime foraging on the beach might be explained as an antipredatory response to nocturnal predators. The avoidance of good roosting sites and profitable feeding areas at night due to the presence of nocturnal avian predators has been hypothesised for several shorebird species. It is the case of Red Knots *Calidris canutus* roosting in the Roebuch Bay, NW Australia (Rogers 2003; Rogers et al. 2006) or feeding in northern Patagonia (Sitter et al. 2001) and Dunlins *C. alpina* roosting in the Yukon Delta in western Alaska (Handel and Gill 1992). Indeed, Piersma et al. (2006) reported conclusive evidence of owl predation on shorebirds. They observed Short-eared Owls *Asio flammeus* actively hunting shorebirds in the Egegik Bay (Alaska) and found freshly remains of a Dunlin in the stomach of an owl. Long-eared Owls *Asio otus* breed in good numbers in the pinewood (see Fig. S2a) adjacent to the beach where our Kentish plovers breed (unpublished data), and they can be potential predators that push female plovers to avoid attending the beach at night and move to the lagoon. Even if direct evidence supporting this hypothesis are still lacking to date, landscape of fear (Laundré et al. 2010) is a possible explanation for the observed nighttime feeding avoidance on the beach. An additional explanation might be found in a possible feeding specialization of females. Even if sex differences in diet have been reported for shorebird species showing body size and/

or bill morphology differences between males and females (Durrell 2003), which is not the case of our studied species, we cannot rule out that Kentish Plover females can benefit from the availability of specific prey items that are available in the lagoon during the night, regardless of tidal conditions. The two hypotheses to explain females' nighttime foraging in the lagoon are not mutually exclusive. Finally, an alternative explanation for the observed sexual difference in foraging behaviour might be that the lagoon is generally a better foraging area even at high tide, but males use semi-optimal periods during high tide for anti-predator and territorial behaviour on the beach.

Kentish Plovers are not colonial breeders, even if they can nest in a loose semicolonial manner (Colwell and Haig 2019). In our study area, nests are generally rather distant from each other (median distance to the closest nest: 92 m, Q1–Q3 40–567 m), thus it is not surprising that incubating birds used foraging areas that were distinctly separated from those used by the others when foraging on the beach. However, some of them seem to prefer specific foraging areas distant from the nest (even several km, Fig. S3). More surprisingly, individuals showed a high individual foraging site fidelity in the Venice Lagoon too, where they relied on foraging sites that were far and unrelated to nesting site (Fig. 1). In the lagoon, each bird consistently foraged in one or few small patches that were very little or not exploited at all by other tagged birds. Although the mechanism generating such spatial segregation of foraging sites in the lagoon is still undisclosed, it is reasonable to assume that this behavioural pattern lowered intraspecific competition for food resources (see Ramellini et al. 2022).

Thanks to GPS-tracking, the present study revealed behavioural patterns of breeding Kentish Plover that would not otherwise be assessed. However, the observed behavioural patterns might be the response to specific local conditions. The Kentish Plover is a cosmopolitan species inhabiting different habitats (Colwell and Haig 2019), and likely evolved a good behavioural plasticity to cope with the different conditions experienced during breeding. An increase in tracking studies on Kentish Plovers breeding in different environments could provide new insights on it.

In addition to the results on the movement ecology of the species, by assessing Kentish Plover foraging sites in the heavily human-impacted beach of Cavallino-Treporti (up to 6 million of tourist every year in 15 km of beach; Ballarin 2018) and in the polluted Venice Lagoon (Frignani et al. 2005; see also Picone et al. 2019), the present study provides solid information that could be useful to address and implement local conservation actions. The species is indeed of conservation interest in Europe (listed in Annex I of EU Birds Directive) and strongly threatened by disturbance of coastal habitats and degradation and loss of

wetlands through environmental pollution (BirdLife International 2022).

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10336-023-02067-7>.

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Author contributions JGC, SI and LS: conceptualized the study. MP, MB, LP, FB, LS and JGC collected the data. SI and JGC analysed data. JGC: wrote the first draft with inputs by SI, MP and LS. All authors read and approved the final manuscript.

Data availability Data used for the analyses are available upon reasonable request from the corresponding author.

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