

Effects of environmental variability and offspring growth on the movement ecology of breeding Scopoli's shearwater *Calonectris diomedea*

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Abstract Most seabird species display colonial behavior during the breeding period which implies that food resources around breeding sites can easily go depleted. Seabirds need to both reach profitable areas, which can be located far from the colony, and return to the colony regularly. In this context, flexibility in movement behavior may be crucial for breeding success. During chick-rearing, Procellariiformes species can alternate short trips lasting 1–4 days for chick provisioning with longer trips for self-provisioning in what has been called a dual-foraging strategy. We analyzed foraging trips from 136 Scopoli's shearwaters from three Mediterranean colonies tracked with GPS during 6 chick-rearing seasons to assess whether the adoption of a dual foraging strategy depends on the quality of habitat surrounding the colony. We found a marked dual-foraging strategy only in birds from the Linosa colony which was the largest colony in terms of breeding pairs and was characterized by having a lower marine habitat quality. Birds from this colony performed foraging trips that extended up to 369 km from the nest and lasted more than 10 days. In general, the decision to perform long lasting trips was triggered by lower values of primary production and higher offspring weight. Contrary to expectation, the decision to feed far from the colony was not related to the parents' weight. At the same time, despite the higher productivity offered by distant areas, the higher proportion of long trips performed by birds breeding in poor areas was not sufficient to maintain the same body mass as the ones breeding in richer areas [*Current Zoology* 60 (5): 622–630, 2014].

Keywords Cory's shearwater, Dual foraging strategy, GPS tracking, Procellariiformes, Seabird

Several of the life-history traits of Procellariiformes, such as the ability to accumulate a large amount of fat, the slow growth of the single offspring, and the prolonged nestling period, are result of adaptations to an unpredictable environment (Ricklefs et al., 1985; Boersma and Parish, 1998). In particular, the difficulty to deliver food to their chick is likely the main reason for the low reproductive rate of these long-lived pelagic seabirds (Lack, 1968; Ricklefs, 1983). During the breeding period, procellariiform species are colonial and central place foragers which implies that food resources around breeding sites can easily go depleted (Ashmole, 1963). Consequently, the accessibility of feeding areas can be inversely related to their distance from the colony (Orians and Pearson, 1979; Matthiopoulos, 2003). During chick-rearing, parents need to match the exigency to reach profitable areas, returning to the colony regularly to feed the chick, and maintaining their own good physical condition at the same time. To face all these

constraints, breeding birds belonging to several procellariiform populations alternate short foraging trips lasting 1–4 days for chick-provisioning with longer trips (>4 days) for self-provisioning in what has been called a dual foraging strategy (Weimerskirch et al., 1994). Adopting this strategy, birds manage to exploit profitable areas located at great distance from the colony every so often (Paiva et al., 2010a; Cecere et al., 2013). It is still debated whether breeding partners are able to coordinate themselves or not in the alternation of short and long lasting foraging trips in order to prevent leaving their offspring unfed for a long period (Magalhães et al., 2008). Despite the alternation of short and long trips by both parents, which implies that food is not delivered to the chick every night, it has been found that in Cory's shearwaters *Calonectris borealis*, both the chick provision rates (grams per night) and the mass growth of the chick are very similar between the colonies where breeders adopt the dual foraging strategy and colonies

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where birds perform only short trips (Magalhães et al., 2008). This means that during long lasting foraging trips, Cory's shearwaters exploit areas so profitable as to allow themselves to both restore their own physical condition and obtain larger meals for their offspring (Grandeiro et al., 1998; Magalhães et al., 2008).

Energy stored by breeders during long trips may cover the costs of searching for food during successive short trips through poorer habitats as has been demonstrated in the Sooty shearwaters *Puffinus griseus* breeding around New Zealand (Weimerskirch 1998) and the Wedge-tailed shearwaters *Puffinus pacificus* breeding in Australia (Congdon et al., 2005).

The dual foraging strategy is described for several Oceanic populations belonging to different procellariiform species and recently for the Scopoli's shearwater breeding in the Mediterranean (Cecere et al., 2013). Nevertheless, a limited number of studies assessed the factors influencing the presence of a dual foraging strategy in a population. Comparing movement patterns of Cory's shearwaters breeding in different Oceanic environments, Paiva et al. (2010b) showed that the dual foraging strategy mainly occurs in colony surrounded by areas characterized by low habitat quality. This evidence is supported by a previous study (Navarro and González-Solís, 2009) which showed that Cory's shearwaters breeding on Gran Canaria, located at 150–250 km (a distance which can be covered in few days by shearwaters) from the high profitable African continental shelf, showed an unimodal distribution of the foraging trip durations. In accordance with this studies, Riou et al. (2011) found that a population of Manx shearwaters *Puffinus puffinus* breeding in SW Walles switched to a dual foraging strategy in 2007 and 2008 contrary to previous years probably as a consequence of a reduction in prey abundance and habitat quality. Within populations adopting the dual foraging strategy, Weimerskirch (1998) showed that in breeding Sooty shearwaters, the decision to perform long trips depends only on the decline of the adult's body mass. On the other hand, Ochi et al. (2010) showed that Streaked shearwaters *Calonectris leucomelas* breeding around Japan this decision also depends on chick body condition, but in the opposite way (i.e. the worst the chick's body condition, the less the number of long foraging excursions their parents perform).

Negative effects of dual foraging strategies on parents have never been investigated. However, since shearwaters use this strategy only under particular conditions, it is reasonable to imagine negative short-term

(e.g., physiological stress, weight) and/or long-term (e.g., survival, lifetime fitness) consequences on breeders.

In this study, we analyzed for the first time to our knowledge, movement patterns of shearwaters during chick-rearing while taking into account both the body mass condition of breeders and offspring and the quality of the habitat surrounding the colony. To pursue this goal, we analyzed foraging tracks from 136 Scopoli's shearwaters breeding in three different Mediterranean colonies.

We approached the topic investigating foraging movements and related physical and habitat conditions at two different scales. At individual scale, we expected long lasting trips to be triggered by lower values of primary productivity around the colony (Riou et al., 2011), good body condition of the offspring (Ochi et al., 2010) and a decrease in parental body mass (Weimerskirch, 1998; Ochi et al., 2010). On the other hand, to investigate the consequences of performing a dual foraging strategy on offspring growth and parental body condition we analyzed foraging movements at population scale. Since long foraging trips should demand higher energetic costs than short trips, we expected the breeders to have a lower average weight in populations performing a higher proportion of long lasting trips, while we did not expect any negative effects on offspring growth (Magalhães et al., 2008).

1 Materials and Methods

1.1 Study areas

The study was carried out during 6 chick-rearing seasons at three Mediterranean colonies: the island of Linosa in 2008, 2009, and 2012, the Tuscan Archipelago in 2010 and 2011, and the La Maddalena Archipelago in 2013 (Fig. 1). Linosa, located in the Tunisian Plateau/Gulf of Sidra region between Sicily, Tunisia, and Libya, hosts one of the biggest colonies of Scopoli's shearwaters in the Mediterranean with an estimated 10000 breeding pairs (Baccetti et al., 2009). The Tuscan Archipelago is located in the Tyrrhenian Sea between Tuscany and Corsica, and on the whole, it hosts 200–500 pairs (Baccetti et al., 2009); the fieldwork was carried out on the islet of La Scola that is the island with the larger number of breeding pairs (60–100). La Maddalena Archipelago is located between Sardinia and Corsica, and it hosts 400–1000 pairs (Baccetti et al., 2009); fieldwork was carried out on the islets of Spargiotto (120–180 pairs) and Baretini (50–100 pairs).

All the fieldwork was carried out between July and August during the early chick-rearing of Scopoli's

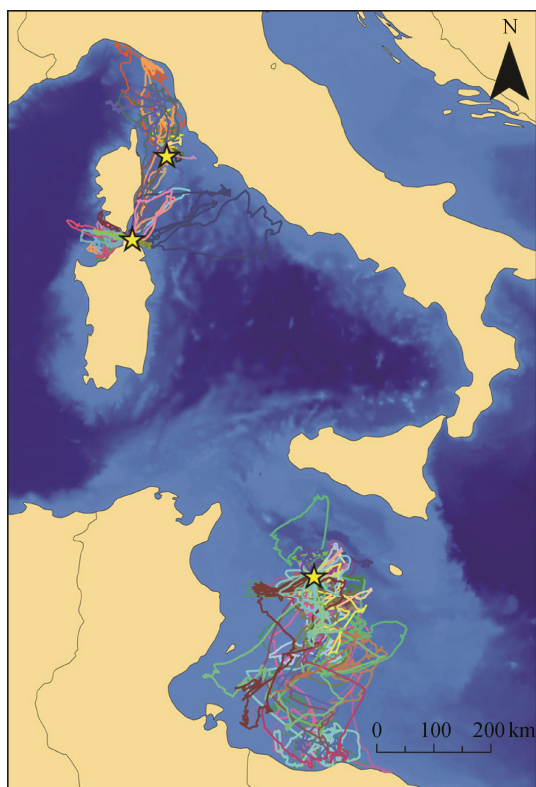


Fig. 1 Foraging trips performed by 83 GPS tracked Scopoli's shearwaters breeding on Linosa island (Southern star), 32 from the La Maddalena Archipelago (Western star), and 21 from the Tuscan Archipelago (Northern star) during chick-rearing

shearwater. In Table 1, we report the starting and ending dates of each field season.

1.2 GPS Logger deployment

We located shearwater nests by inspecting crevices and burrows. Breeding birds were caught at night just after they had fed their chick. Birds were weighed and sexed by using their sex-specific vocalizations or by the sex determination of their partner. The mini-GPS logger was attached to the back feathers using 3–4 strips of Tesa® marine cloth tape (Tesa SE, Hamburg, Germany). We used three types of mini-GPS loggers: one by Earth

& Ocean Technologies (Kiel, Germany) weighing 19.4 grams (with a battery of 500 mA) and two different types by Technosmart (Guidonia, Italy) weighing 11.9 and 9.8 grams with two different batteries (500 and 250 mA respectively). The deployment of lighter GPS loggers allowed us to track lighter birds despite the shorter life-span of these devices. Device weight was always less than 3% of the bird's weight, following current recommendations (Phillips et al., 2004; Passos et al., 2010). All GPS loggers were configured to record both the position and the instantaneous speed of the bird every 10 minutes.

Before releasing a tagged bird, we weighed its chick. Total handling time was kept below 10 minutes, and birds were returned to their nests immediately afterwards. Since adults normally spent little time in their burrow, it was not always possible to re-capture the equipped bird after the first foraging trip; hence, more than one trip might have been recorded for a given bird. Nevertheless for all analyses, we only considered the first trip of each bird.

1.3 Environmental data

It is well known that both chlorophyll a concentration and sea surface temperature affect marine phytoplankton productivity which in turn influences the feeding behaviour of pelagic birds (Wakefield et al., 2009). We chose to use the net primary production data (standard VGPM) which is based on monthly MODIS-aqua R2013.1 input data including sea surface temperature, chlorophyll, and photosynthetically active radiation values (Behrenfeld and Falkowski, 1997). Net primary production data was downloaded from the Ocean Productivity site (<http://www.science.oregonstate.edu/ocean.productivity/index.php>) for a spatial resolution of 10 minutes (approx. 18 km).

To investigate sea productivity in an area that could be potentially explored by breeding birds in a short time, we drew a 60 km buffer around the different colonies in accordance with Paiva et al. (2010c) and based on the

Table 1 Summary data of the six field seasons

Colony	Sampling year	date		No. trips	Long trips	Long Trip Area Kernel (km ²)	Overlap	No. weighed chick
		start	end					
Linosa	2008	20-July	30-Aug	18	39%	45407	14%	4
Linosa	2009	17-July	11-Aug	28	14%	23624	31%	16
Linosa	2012	21-July	10-Aug	37	19%	50924	16%	28
Tuscan Arch.	2010	11-Aug	17-Aug	10	20%	15063	34%	9
Tuscan Arch.	2011	22-July	28-July	11	9%	9970	48%	5
La Maddalena Arch.	2013	17-July	30-July	32	6%	16606	6%	19

median Euclidian distance reached during short trips (≤ 4 days, median=53.66 km, $n=114$). Since the two islets of La Maddalena Archipelago were very close (7.13 km), we drew only one buffer around the halfway point. Mainland and islands were excluded from the buffer areas. We then created a series of random points inside the buffer areas with a fixed density of 0.01 points per km^2 (113 for Linosa, 105 for Tuscan Archipelago, and 71 for La Maddalena). For each point we extracted the value of net primary production corresponding to the month during which the tracking study was carried out. However, of the 620 total random points, only 605 were actually associated with a primary production value due to the characteristics of the VGPM raster. For Linosa, we extracted the value of both July and August from the three field seasons, and for each point, we calculated the mean value of primary production between the two monthly values. However, since trips were not recorded uniformly throughout each season, the mean value of each point was weighted for the proportion of departure dates in the two months. Finally, we calculated the mean value of net primary production for each field season and colony, and we used this value for successive analyses.

1.4 Kernel analyses

Following previous experience from BirdLife International partners (see Ramirez et al., 2008), we computed kernel analyses using only GPS positions with an instantaneous speed of less than 10 km/h. This threshold has been used for shearwaters (for Scopoli's shearwaters see Cecere et al., 2012) to identify positions where birds were actually using the environment for either resting, searching for food, or diving and excluding positions where the bird was travelling. We only computed the kernel analysis for data from trips lasting more than 4 days in order to identify areas exploited by breeders during long excursions. Kernels were computed with the Home Range Tool 1.1 (Rodgers et al., 2007) for ArcGis 9.3 (ESRI®) and using the 95% fixed kernel density (Worton, 1989). To compare outcomes from different colonies, we used the same scale to perform fixed kernel analyses by using the same value of smoothing parameter (bandwidth, h) for the calculation of kernels for each field season. After inspecting several possibilities, we chose the smoothing factor ($h=10,000$) that computed 95% fixed kernel density which better encompassed the GPS positions while keeping the number of different polygons of a single kernel as low as possible. Then, we calculated the percentage of its area overlapping the 60 km-buffer around the colony for

each kernel. All spatial analyses have been performed using Esri ArcGIS 9.3.

1.5 Statistical analyses

Since both the percentage of long lasting trips and the area covered during long trips are both positively related to the number of days from hatching (Cecere et al., 2013), we corrected the two former variables by calculating the residuals of the regressions with the average Julian departure date (for simplicity, the number of days from July 1st) of the tracked breeders in each field season.

To investigate the different movement strategies during short trips, we calculated a modified version of the Tortuosity index (Lane, 1957). The original index reads as $T=L/C$, where L is the total length of the path and C is the distance between the ends of it. However, since birds start and end their trip at the same point, we used the index $T=L/D$, where D is the maximum Euclidean distance from the colony reached by the bird during the trip. To avoid problems due to the different duration of trips, we considered only 1-day trips, which represent 61% of all short trips (66 out of 109).

We then calculated the Spearman correlation coefficient between the average primary productivity within the 60 km-buffer around the colonies for each field season and the following variables: the proportion of long lasting trips corrected for the average departure date, the area of the 95% kernel of long trips corrected for the average departure date, the percentage of the 95% kernel of long trips overlapping the 60 km-buffer around the colony, the average Euclidian distance from the colony reached by birds during long trips (> 4 days), the average distance from the colony reached during 1-day trips, and the average Tortuosity index of 1-day trips.

To assess which factors affected the decision to perform a long trip at individual scale, we performed a series of Generalized Linear Mixed Models (GLMM) using the duration of the trip of each tracked bird as a binomial dependent variable (0: 1–4 day long trip, 1: > 4 day long trip) and the average primary productivity within the 60 km buffer during the corresponding field season, the weight and sex of the breeder, and the weight of the chick as independent variables. Since Julian date was highly correlated with the chick's weight, we did not consider the former variable as of lesser biological significance. Colony was first entered as a random effect in the complete model, and it was compared to the complete model without random factors (Zuur et al., 2009). We then used AIC (Burnham and Anderson, 2002) for model selection. The best per-

forming models with $\Delta\text{AIC} \leq 6$ (Richards, 2005) were used to perform model averaging with the corresponding Akaike weights (Burnham and Anderson, 2002).

Finally, at population scale, we used Generalized Linear Models (GLM) to investigate the relationships between the percentage of long lasting trips performed during each season (corrected for the average departure date of tracked breeders) and the weight of the chick (corrected for departure date of the parent) and between the corrected percentage of long lasting trips and the weight and sex of each breeder, as well as, the interaction between the two latter variables. All analyses were performed in R ver. 2.15.3 (R Core Team 2012), with the “lme4” package (Bates et al., 2012) for GLMMs and the “MuMIn” package (Barton, 2013) for model averaging.

2 Results

We recorded a total of a 136 tracks from as many breeding birds (83 from Linosa, 21 from Tuscan Archipelago, and 32 from La Maddalena Archipelago) (Fig. 1). The percentage of long trips (> 4 days) was higher on average for Linosa birds and lower for La Maddalena Archipelago birds (Table 1). Shearwaters from Linosa covered larger areas during their long trips (kernel 95%) that had a 20% average overlap with the 60 km-buffer around the colony. On the contrary, shearwaters from the Tuscan Archipelago covered the smallest areas with a 41% average overlap (Table 1). The smallest overlap (6%) was recorded for La Maddalena birds but was based on only two long trips. The number of weighed offspring was lower than that of tracked breeders, since not every burrow allowed us to catch the chick (Table 1). Additionally, the sample in 2008 was particu-

larly smaller than tracked breeders since we weighed most of the chicks several days after GPS deployment on adults, but we didn't consider these data for the analyses.

2.1 Foraging strategies vs primary productivity

Primary productivity was significantly different among field seasons (ANOVA, $F = 287.59$, $df = 5$, $P < 0.0001$). The post-hoc Tukey test showed statistically significant differences between all pair-wise comparisons except between the La Maddalena Archipelago and the Tuscan Archipelago in 2010 and between Linosa in 2009 and 2012. The area surrounding the Linosa colony was characterized by lower average values of primary production (Fig. 2).

The residuals from the regression between the percentage of long lasting trips (as well as the area size covered during long trips) and the average bird departure date during each field season were both negatively correlated with average primary productivity (% long trips: $r_{\text{spearman}} = -0.83$, $P = 0.04$, $n = 6$; Kernel 95% long trips: $r_{\text{spearman}} = -0.94$, $P = 0.005$, $n = 6$) (Fig. 3A, B). The overlap between the 95% kernels and the 60 km-buffer around the colony was positively related to primary productivity, but the relation was not significant ($r_{\text{spearman}} = 0.66$, $P = 0.16$, $n = 6$) likely due to the small sample size (6 points) and the La Maddalena Archipelago outlier (Fig. 3C). The average Euclidian distance from the colony reached by birds during long trips in each season was negatively related to the primary productivity of the colony surrounding area but non-significant ($r_{\text{spearman}} = -0.60$, $P = 0.21$, $n = 6$) likely for the same reasons (Fig. 3D). On the contrary, there was no relationship between the average distance from the colony reached during the shortest trips (1 day) and primary productivity ($r_{\text{spearman}} = 0.03$, $P = 0.96$, $n = 6$), but

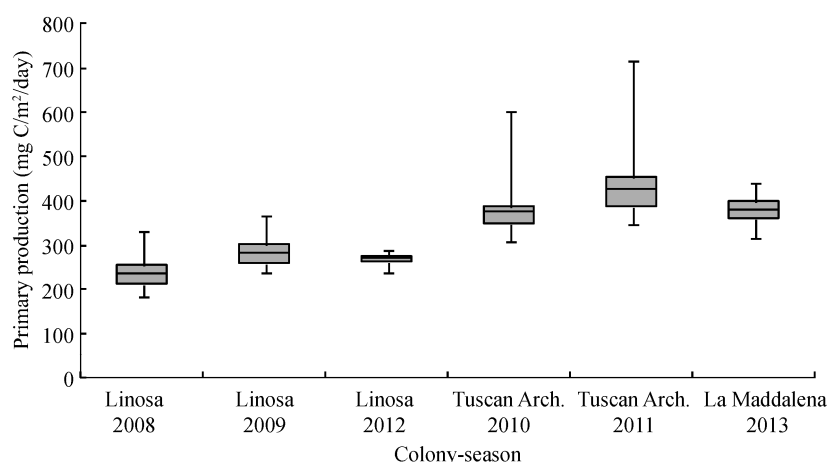


Fig. 2 Boxplots (median, interquartile range, and min-max values) of average primary productivity within the 60 km buffer around the three colonies during the six field seasons

the average tortuosity index of 1-day trips was significantly higher with higher primary productivity around the colony ($r_{\text{spearman}} = 0.94, P = 0.005, n = 6$) (Fig. 3E, F).

2.2 Factors affecting the decision to perform long lasting trips

In regards to the models performed at individual scale with the binomial trip duration (short/long) as dependent variable and all the considered fixed factors,

the one including colony as random effect showed a better fit than the model without it ($\Delta\text{AIC} = 8.05$); therefore the former random structure was selected for the successive analyses. Four models showed a $\Delta\text{AIC} \leq 6$ (Table 2). Averaged coefficient estimates showed that the decision to perform long trips depended on lower values of primary productivity around the colony and a greater weight of the offspring (Table 3).

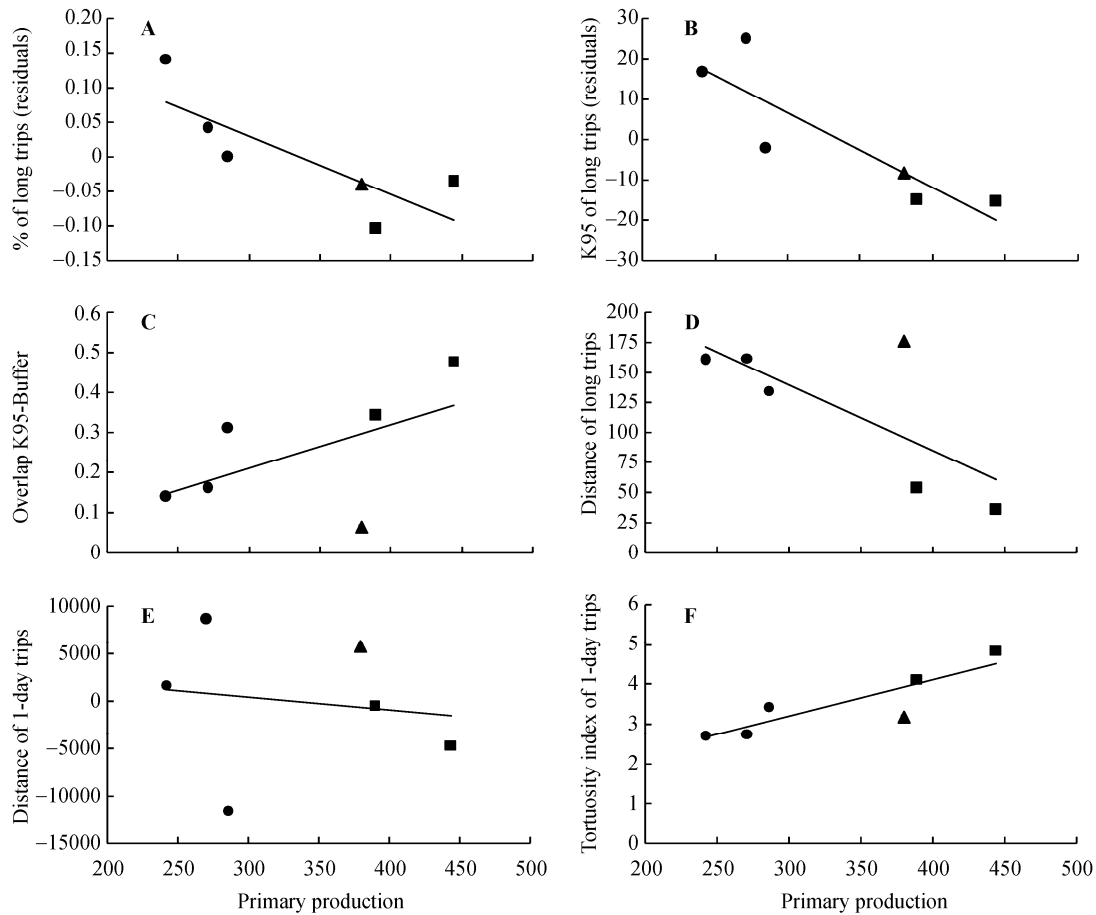


Fig. 3 Relationship between the average primary productivity within the 60 km-buffer around the colony and (A) the proportion of long lasting trips corrected for the average departure date, (B) the area of the 95 % kernel of long trips corrected for the average departure date, (C) the percentage of the 95% kernel of long trips overlapping the 60 km-buffer around the colony, (D) the average Euclidian distance from the colony reached by birds during long trips, (E) the average distance from the colony reached during 1-day trips, and (F) the average tortuosity index of 1-day trips
Circles: Linosa colony; squares: Tuscan Archipelago; triangle: La Maddalena Archipelago.

Table 2 Logistic GLMMs performed with the kind of trip (Short/Long) for each tracked breeding bird

	Model (Short/Long trip)	AIC	ΔAIC	w_i
1	Sex + Weight_chick + PrimProd + (1 Colony)	58.96	0.00	0.41
2	Weight + Weight_chick + PrimProd + (1 Colony)	59.77	0.82	0.27
3	Weight + Sex + Weight_chick + PrimProd + (1 Colony)	60.77	1.82	0.16
4	Weight_chick + PrimProd + (1 Colony)	60.88	1.93	0.16

Weight: body mass (gr) of the breeder; Sex: gender of the breeder; Weight_chick: body mass of the chick at the departure of the parent; PrimProd: average net primary productivity ($\text{mg C m}^{-2} \text{day}^{-1}$) within the buffer surrounding the colony in the tracking season. Colony, in brackets, was entered as random effect. All models with $\Delta\text{AIC} \leq 6$ are showed.

Table 3 Model averaging for the kind of trip (Short/Long) of each tracked bird

	Coeff. estimate	<i>z</i> value	<i>P</i>
Intercept	4.46 ± 4.97	0.90	0.37
Weight_chick	0.58 × 10 ⁻² ± 0.25 × 10 ⁻²	2.31	0.021
PrimProd	-0.22 × 10 ⁻¹ ± 0.84 × 10 ⁻²	2.65	0.008
Sex	1.37 ± 0.91	1.50	0.13
Weight	-0.90 × 10 ⁻² ± 0.92 × 10 ⁻²	0.98	0.33

The averaged parameter estimates of all variables included in the models with $\Delta\text{AIC} \leq 6$ (Richards 2005) are weighed with the corresponding Akaike weight. Names of variables as in Table 2. Significant *p*-values are in bold

2.3 Effects of adopting dual foraging strategy

At population scale, despite a slightly negative tendency, there was no significant relationship between the weight of the chick and the percentage of long lasting trips performed during each season (both corrected for the departure date of each breeder) ($F = 0.77$, $r^2 = 0.01$, $df = 80$, $P = 0.38$) (Fig. 4A). On the contrary, the weight of the breeders of both sexes was negatively related to the percentage of long lasting trips corrected for the departure date, but there was no significant interaction between this latter variable and sex ($F = 44.19$, $r^2 = 0.51$, $df = 132$, $P < 0.001$; % long trips: $F = 6.22$, $P = 0.01$; sex: $F = 125.29$, $P < 0.0001$; % long trips*sex: $F = 1.07$, $P = 0.30$) (Fig. 4B).

3 Discussion

During the breeding season, many procellariiform populations alternate short trips for chick provisioning with long lasting trips mainly performed for self-provisioning (Weimerskirch et al., 1994; Weimerskirch, 1998; Congdon et al., 2005; Magalhães et al., 2008). We investigated factors affecting the movement ecology of Scopoli's shearwaters breeding in three different Mediterranean colonies during chick-rearing, and we showed

that the proportion of long lasting trips within a chick-rearing season was higher when the area surrounding the colony was characterized by lower values of primary production. Moreover, we showed that the decision to perform a long trip during the course of a breeding season depended both on the marine productivity around the colony and the offspring's body mass. At the same time, the adoption of the dual foraging strategy over all the breeding season was associated with lower parental body mass.

In accordance with a previous study on Manx shearwaters (Riou et al., 2011), we found that habitat quality is a key factor for the dual foraging strategy. Linosa was the colony characterized by lower values of marine primary production, and birds from this colony were the ones which performed the highest proportion of long lasting trips. This became clearer when considering the effect of the departure date, since it was demonstrated that the proportion of long trips performed by Scopoli's shearwaters increases as the chick-rearing season proceeds (Cecere et al., 2013). Similarly to what happens to Cory's shearwater in the Atlantic Ocean (Paiva et al., 2010c), the percentage of long trips corrected for the study period decrease with increasing primary productivity around the breeding site. While performing long lasting trips, Scopoli's shearwaters forage farthest from the colony, and they exploit larger areas (Cecere et al., 2013). But in addition, our data showed that with a lower quality of the habitat surrounding the colony, breeders used long lasting trips to exploit areas that are larger, located at a greater distance from the nests, and have a smaller overlap with the area nearby the colony. Flexibility in movement behavior may be crucial for seabirds to access food resources (Wilson et al., 2005; Hammer et al., 2007), and shearwaters have a good ability to change their search strategy when faced with biological and ecological constraints (Focardi and

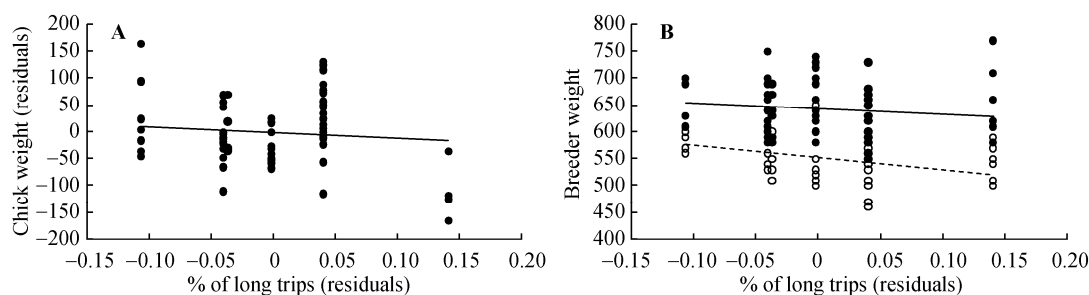


Fig. 4 Relationship between the proportion of long lasting trips corrected for the average departure date and (A) the weight of the chicks corrected for the weighing date and (B) the weight of the tracked breeders

Black dots: males; empty circles: females.

Cecere, 2014). At the short trip scale, birds performed more tortuous paths when ranging in habitat characterized by higher values of primary production, which is likely a consequence of active food searching. This evidence highlights the influence of habitat quality around the breeding site on the movement ecology of Scopoli's shearwaters even at a small spatial scale. The spatial match between marine productivity and seabird distribution is well demonstrated by several studies (e.g., Grémillet et al., 2008). Despite seabirds do not feed on phytoplankton, many studies showed that marine ecosystems are controlled via bottom-up processes (Frank et al., 2007) and the lowest trophic level of a marine food web can match with the highest (Grémillet et al., 2008).

Contrary to Weimerskirch (1998), we did not find any evidence that the decision to perform a long trip depends on the adult body mass. Besides habitat quality, we found that long trips of breeding individuals were triggered when chicks had a higher weight, similarly to what Ochi et al. (2010) found for the con-generic Streaked shearwater. Usually in birds, long fasting periods during the first days after hatching may cause detrimental effects on intestine development and a serious delay in chick growth, while it is less serious at later times (Geyra et al., 2001). Our results suggest that until the chick is at first growth stage, or it is found in poor condition, it is fed frequently inducing parents to ignore their own condition. The increasing body mass of the chick may allow parents to perform long trips for self-provisioning. This is of course the situation which happens when the colony is surrounded by low habitat quality, otherwise breeding birds can take on food for both themselves and offspring performing short trips.

The evidence that the proportion of long trips among field seasons was related to habitat quality suggests that, if possible, shearwaters prefer to forage nearby the colony, and in accordance to Magalhães et al. (2008) we did not find any negative effects on offspring growth. Nevertheless, we can not exclude a negative consequence on parent fitness. Despite the weight of the parent did not influence the decision to perform a long trip, our results showed that a breeding season characterized by a marked dual foraging strategy is associated with a lower body mass of the breeders at population scale. Parents may be forced to fast for several days during successive short trips and then to cover great distances to restore energy reserves. Despite the fact that long lasting trips allow shearwaters belonging to different populations to exploit much more profitable areas (Paiva et al., 2010a;

Cecere et al., 2013), our data showed that the higher proportion of long trips performed by birds breeding in poor areas was not sufficient to maintain the same body mass as the ones breeding in richer areas. To the best of our knowledge, this is the first study which analyzes the effect of adopting the dual foraging strategy on breeding seabirds. However, further studies are necessary to better analyze potential physiological costs on breeders or carry-over effects from the alternation of short and long lasting trips during chick-rearing on the non-breeding behaviour and on the breeding success in the following season (Catry et al., 2013).

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