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BEHAVIORAL ECOLOGY - ORIGINAL RESEARCH

# Fine-scale spatial age segregation in the limited foraging area of an inshore seabird species, the little penguin

**Laure Pelletier · André Chiaradia · Akiko Kato · Yan Ropert-Coudert**

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**Abstract** Competition for food resources can result in spatial and dietary segregation among individuals from the same species. Few studies have looked at such segregations with the combined effect of sex and age in species with short foraging ranges. In this study we examined the 3D spatial use of the environment in a species with a limited foraging area. We equipped 26 little penguins (*Eudyptula minor*) of known age, sex, and breeding output with GPS (location) and accelerometer (body acceleration and dive depth) loggers. We obtained dietary niche information from the isotopic analysis of blood tissue. We controlled for confounding factors of foraging trip length and food availability by sampling adults at guard stage when parents usually make one-day trips. We observed a spatial segregation between old (>11 years old) and middle-aged penguins (between 5 and 11 years old) in the foraging area. Old penguins foraged closer to the shore, in shallower water. Despite observing age-specific spatial segregation, we found no differences in the diving effort and foraging efficiency between age classes and sexes. Birds appeared to target similar prey types, but showed age-specific variation in their isotopic niche width. We hypothesize that this age-specific segregation was primarily determined by a "cohort effect" that would lead individuals sharing a common life history (i.e. having fledged and dispersed around the same age) to forage preferentially together or to share similar foraging limitations.

**Keywords** Chick-rearing · Cohort effect · Foraging 'hot-spots' · Prey-predator interactions

## Introduction

Colonial living confers benefits as it may provide protection against predators or could enhance mate-choice (reviewed in Andersson 1994). However, a large aggregation of individuals, whether it consists of a single species or several species using similar habitats, can lead to resource limitation and may limit the available space for breeding. If individuals in the aggregation have similar energy requirements and exploit the same trophic niche, this may constrain their access to food resources (Pianka 1981; Furness and Birkhead 1984; Keddy 1989).

Central-place foragers commute between their breeding site and the foraging grounds on a regular basis and are limited in their foraging range by their travelling capacities. Competition for food can be particularly acute for central-place foragers that live in dense colonies. This competition for resources may affect an individual's foraging success, which will have consequences for reproduction, and ultimately survival (Schoener 1986). In the presence of resource limitation, animals should thus modify their foraging behaviour to reduce competition in order to maximize

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L. Pelletier · A. Kato · Y. Ropert-Coudert
CNRS, UMR7178, 67037 Strasbourg, France

L. Pelletier (✉) · A. Kato · Y. Ropert-Coudert
Université de Strasbourg, IPHC, 23 rue Becquerel,
67087 Strasbourg, France
e-mail: laurepelletier@yahoo.fr

A. Chiaradia
Research Department, Phillip Island Nature Parks, Cowes, VIC,
P.O. Box 97, 3922, Australia

their fitness (Pianka 1981; Bolnick et al. 2003). To reduce the extent of competition, individuals, populations, and communities can partition the use of resources by exploiting different habitats (Schoener 1986) at different times (e.g. Alanärä et al. 2001; Kronfeld-Schor and Dayan 2003), and/or by modifying their dietary preferences (e.g. Bocher et al. 2000).

Individual characteristics (e.g. sex, age, body condition) favour the partitioning of resources in space and time. Among the characteristics, sex and body size have probably received the most attention in the literature (Phillips et al. 2004; Page et al. 2006; Stauss et al. 2012). Segregation often results from social dominance and competitive exclusion, or from niche specialisation (Pianka 1981). Sex-specific segregation may occur when differences in morphology (sexual dimorphism) confer a higher manoeuvrability like in the smaller males of the American kestrel *Falco sparverius* (Ardia and Bildstein 1997), or when sex-specific reproductive roles command for different foraging strategies like in the females of New Zealand fur seals *Arctocephalus forsteri* that use a different habitat than the males during their relatively brief foraging trips (Page et al. 2006). In diving marine top predators, including seabirds, the spatial segregation can further expand to the vertical dimension as individuals can use different portions of the water column in relation to differential diving capacities that are related to differences in body size. For instance, larger male cormorants, *Phalacrocorax* spp., dive deeper than smaller females to access higher trophic level prey items (Bearhop et al. 2006).

Age-specific foraging skills could also lead to foraging segregation as age-specific requirements could result in a specialization for specific food resources, but also through two processes: acquisition of experience at young ages and decline in physical capacities at old age (senescence, see Clutton-Brock 1988). Young individuals may indeed not be skillful enough to track high quality food resources, or they could be excluded from using the best feeding sites by the older and more experienced individuals (Wunderle 1991; Sol et al. 2000). The acquisition of foraging skills at young ages is generally rapid and of great magnitude. In fact, a substantial number of studies have investigated the behavioural (e.g. Daunt et al. 2007) and physiological mechanisms underlying the learning processes (e.g. Ponganis et al. 1999). In contrast, the study of the foraging efficiency of senescent individuals, i.e. individuals that present a gradual decrease in reproductive success (e.g. Angelier et al. 2006; McCleery et al. 2008) or reduced physiological abilities (Hausmann et al. 2005; Vleck et al. 2007), have received comparatively less attention (but see the decline in activity levels of old individuals noted by Catry et al. 2006, 2011; Lecomte et al. 2010). It would thus be particularly interesting to compare the foraging activity of birds at different age classes in order to highlight the effect of senescence in free-living individuals. In addition to this, a combination of size, sex, and age could result in spatial (horizontal or vertical) and/or dietary segregation, but this has been rarely combined in one study, at least in long-lived marine vertebrates. The influence of sex and age have been demonstrated in the wandering albatrosses *Diomedea exulans* and their large foraging range (Weimerskirch et al. 1997; Lecomte et al. 2010). Although we can expect competition for resources to be stronger for species with a restricted foraging range, little information is available for species with short foraging range.

Using the little penguin *Eudyptula minor* as a model species we investigated whether inshore seabirds segregate resources according to sex- or age-specific characteristics. The study was conducted in a year of high breeding success where 1.7 chicks fledged per pair, indicating high food availability in that year (Chiaradia and Nisbet 2006). In years of low food availability, the number of fledged chicks drops to less than 0.7 chicks per pair (Daniel et al. 2007). During the chick-rearing phase, little penguins typically make one-day foraging trips (Chiaradia and Kerry 1999), within a 30 km radius of their breeding site (Collins et al. 1999). As visual hunters (Cannell and Cullen 1998), they are further restricted to hunting during daylight hours (Chiaradia et al. 2007). We expect these constraints to result in intraspecific resource partitioning despite abundant prey availability. As little penguins exhibit little sexual size dimorphism, with the main sexual differences being found in bill size and shape (Arnould et al. 2004), we hypothesize that age is a stronger driver of the foraging behaviour than sex. If differential exploitation of resources is observed, we expect middle-aged birds to show greater foraging efficiency (see Zimmer et al. 2011a) than older birds that should show senescence related to decrease in performance.

## Materials and methods

The study was carried out at Phillip Island, Victoria, Australia (38°31′S, 145°09′E), which contains a population of approximately 28,000–32,000 breeding adults (Sutherland and Dann 2012). A subset of the Penguin Parade® colony with 100 artificial nest boxes (details in Chiaradia and Kerry 1999) have birds identified with passive RFID transponders (Allflex, Australia). The transponders (23 × 3.8 mm), supplied in individually packed sterilized needles, were injected under the loose skin between the shoulders before chicks fledged, with the wound sealed with surgical glue (Vetbond™, 3 M worldwide) to prevent infection and transponder loss (details in Chiaradia and Kerry 1999). Transponders have been used at Phillip Island since 1994 and no negative effects have been noted, i.e. no tissue damage or transponder migration from the injected site (Daniel et al. 2007). Age was calculated in round years by subtracting the date of marking to the year of breeding. Birds were sexed by bill measurements (Arnould et al. 2004).

Between October and November 2010, we monitored the foraging activity of 26 known-age penguins (13 males and 13 females, Annexe 1) guarding one or two chicks aged from 1 to 19 days over a single trip.

Birds were caught in their nest boxes and weighed to the nearest 10 g using a spring balance. Adult ages ranged from 5 to 18 years (the oldest birds in Phillip Island were 25 years old, Dann et al. 2005). For the analyses, penguins were grouped into two age classes following Daniel et al. (2007): middle-aged (5–11 years, $n = 11$; seven females and four males) and old penguins (12–18 years, $n = 15$; six females and nine males). These age groups were determined following the quadratic relationship between age and breeding success (Nisbet and Dann 2009) and were then used to examine age effects on diving parameters of little penguins (Zimmer et al. 2011a). Middle-aged birds had higher and more stable reproductive success compared to old and senescent penguins (Daniel et al. 2007; Nisbet and Dann 2009).

GPS receivers and accelerometer data loggers were attached to the middle and lower back of penguins using waterproof TESA® tape (Beiersdorf AG, GmbH, Hamburg, Germany) preserving the integrity of the plumage and allowing us to minimize the handling time (Wilson et al. 1997). The two devices together weighed ca. 39 g in total, which is 3.4 ± 0.3 % of the penguins' mean body weight and 4.1 % of the lightest bird. This ratio is on the upper limit of logger/body mass ratio recommended in the literature (Ropert-Coudert et al. 2007). Logger attachment was completed within 5 min, and penguins were returned to their nest boxes immediately after deployment (details in Zimmer et al. 2011a). After a single foraging trip, penguins were recaptured and loggers were retrieved. Around 150 µL of blood was collected from the tarsal vein (see Chiaradia et al. 2010 for blood sampling details). The fieldwork protocol was approved by the Phillip Island Animal Experimentation Ethics Committee (all procedures were conducted under permits 2.2010 and 3.2011) with a research permit issued by the Department of Sustainability and Environment of Victoria, Australia (number 10006148).

## Foraging activity measurement

We used miniature (12 × 45 mm) five-channel accelerometer data loggers that weighed 9 g (ORI400-D3GT, Little Leonardo, Tokyo, Japan) to record depth (range 0–400 m, resolution 0.1 m) and temperature (range −50 to 50 °C, accuracy 0.1 °C) every second. This logger also recorded both specific acceleration (dynamic) and gravity-related acceleration (static) along the longitudinal body axis (surge), the dorso-ventral axis (heave) and the lateral axis (sway) of the penguins, between −40 and 40 $\mathrm{m\ s^{-2}}$ at 50 Hz.

Data from the accelerometer loggers were downloaded and analysed with purpose-written software in Igor Pro (Wavemetrics Inc., USA, 2008, Version 6.22A, see Kato et al. 2006). Based on the accuracy of the depth sensor and wave effect at the surface (Kato et al. 2006), dives started when a penguin descended at least 1 m from the water surface and ended once the penguin surfaced again. Using this method, we calculated the total number of dives performed during the foraging trip, the total vertical distance travelled (the sum of the maximum dive depth × 2), as well as the proportion of time spent underwater.

The Vectorial Dynamic Body Acceleration (VeDBA), a measure of the whole body activity, was derived from the acceleration along the three axes (Gleiss et al. 2011). Specific and gravity-related acceleration signals were separated by a two-band low-pass filter (IFDL, Version 4, Wavemetrics) on each acceleration axis (surge, heave and sway). The gravity-related acceleration was subtracted from the total acceleration in order to obtain the specific acceleration. The vectorial sum of the three axes' specific accelerations was calculated to give the VeDBA. During prey pursuit, the frequency and amplitude of flipper beat increases (Ropert-Coudert et al. 2006), resulting in a peak in VeDBA (Gleiss et al. 2011; Zimmer et al. 2011b). Although this method does not provide a direct measure of prey consumption, it does give a good estimate of food available to a penguin during a trip. We calculated the ratio of the number of dives with prey pursuit to the total number of dives during the foraging trip, as an index of hunting efficiency (Zimmer et al. 2011a, b).

## Tracking devices and spatial analysis

Penguin location at sea was recorded using CatTraQ™ GPS loggers (16 Mb memory, 230 mA lithium-ion battery, Catnip Technologies, USA). These GPS loggers were modified in our laboratory (IPHC–DEPE, Strasbourg, France) for underwater use. The initial packaging was removed, the main switch button replaced by a reed switch, and the units were then moulded into a resin casing. After sampling protocol was uploaded, each unit was waterproofed inside a heat-shrink tube before deployment. Dimensions of the customized unit were 14 × 35 × 70 mm, weighing ca. 30 g. The GPS loggers were set to record from 3 am to 9 pm local time, with a 15-s sampling interval. All GPS track records were analysed using IGOR Pro with the

'*Spatial analysis*' function of the *Ethographer* (version 2.0; Sakamoto et al. 2009) and R software 2.11.1 (R Development Core Team 2011). Geographic coordinates from GPS loggers were transformed in UTM (Universal Transverse Mercator) values. The signal between the satellites and the devices were interrupted every time birds were underwater. To correct for irregular interval between satellite fixes, tracks were linearly interpolated at a rate of one point per minute. The maximum foraging distance and major heading directions were calculated as the distance (in km) and bearing (degree from north) to the furthest point in the trip from the colony. We also calculated the total distance travelled during each foraging trip as the cumulative distance between each point (in km).

Using data from the accelerometer loggers combined with GPS data, we plotted the locations of prey pursuits onto the tracks for each penguin. To determine overall patterns of spatial foraging distribution, we calculated Kernel density (Worton 1989) to determine the zone of prey pursuit for each age class and each sex using the *KernelUD* function in R package *adehabitat* (Calenge 2006). We used the smoothing factor and grid cell of 7 and 2 km, respectively. Areas of high density of prey encounter ('hot-spot' foraging areas) for the 25 % (core area) and 50 % (focal area) were calculated for each age class and each sex (Hyrenbach et al. 2002; Kappes et al. 2011). The overlap between the groups, in the 25 and 50 % areas of the foraging range were calculated using R command *Kerneloverlap* with the *VI* method (Fieberg and Kochanny 2005). This method computes the proportion of the volume of intersection between groups. We calculated the surface area (in km$^2$) used by each group, at 25 and 50 %, using the *kernel.area* command in R package *adehabitat* (Worton 1989; Calenge 2006). Finally, we added published bathymetry data (Whiteway 2009) to determine the depths in the penguins' foraging zones.

## Stables isotopes

Blood samples were centrifuged, and the red cells and plasma were frozen (−20 °C) separately until further analyses in the laboratory (IPHC-DEPE, Strasbourg, France). The stable isotopic ratios of carbon ($\delta^{13}$C, $^{13}$C/$^{12}$C) and nitrogen ($\delta^{15}$N, $^{15}$N/$^{14}$N) estimate the penguins' foraging locations (levels of $\delta^{13}$C are related to benthic/inshore prey) and the trophic position of the predator (values of $\delta^{15}$N are related to trophic position of consumed prey) (Hobson and Clark 1993; Cherel and Hobson 2007). The isotope ratios were measured in the plasma, which provides a composite of prey consumed in the last 5 days for an animal of similar body mass (~ 1 kg) of little penguins (Hobson and Clark 1993). Results are presented in the δ notation (‰) following international standards (PeeDee Belemnite for $\delta^{13}$C and atmospheric nitrogen for $\delta^{15}$N). Lipids were extracted from plasma using cyclohexane solvent (Cherel et al. 2010). Each sample was lyophilized (48 h), powdered, and weighed with a microbalance (0.22–0.95 mg), and the material was loaded into tin cups for analysis. Replicate measurements of internal laboratory standards indicate measurement errors of ± 0.19 and ± 0.08 ‰ for $\delta^{13}$C and $\delta^{15}$N, respectively.

## Statistics

To identify any horizontal, vertical, and isotopic diet segregation in relation to the effect of age class, sex, and/or the interaction between sex and age class, we tested these parameters on the bearing and the stable isotope values using generalised linear modelling (GLM) with a gamma distribution. Age could not be treated as a continuous variable given the unequal sample sizes between groups. We, therefore, treated age as categorical variable grouped into two age classes, middle-aged and old birds (Daniel et al. 2007). For maximum depth of dives with prey pursuit and the seabed depth we tested the age and sex parameters using generalised linear mixed modelling (GLMM) with a Gaussian distribution and individuals as a random factor given that each individual performed several dives within the 1-day foraging trip. All analyses were conducted using R 2.11.1 (R Development Core Team 2011) with the *nlme* package (Pinheiro et al. 2013). Results are expressed as mean ± SE and significance level set at $\alpha = 0.05$.

We used the following foraging parameters to characterise foraging effort: the number of dives performed during the foraging trip, the percentage of time spent underwater, the total vertical distance travelled, the maximum distance reached from the colony and the total horizontal distance travelled. To define the efficiency of a foraging trip we used the index of hunting efficiency (i.e. the proportion of dives with prey encounter). Using GLMs, we tested the effect of the following individual parameters on foraging effort parameters: age class (Middle–Old), sex, body mass, the interaction between sex and adult age classes, as well as chick's growth requirement (represented by the age of the chick), and the date, which although not a characteristic of the individual adults per se, are known to be related to their foraging effort (Zimmer et al. 2011b). Response variables followed different distributions: Poisson for the maximum and the total horizontal distance travelled and the total vertical distance; negative binomial for the total number of dives; binomial for time spent underwater (%); and hunting efficiency.

We used model selection to choose the best-fitted models with GLM, using AICc and Akaike weight ($w_i$)

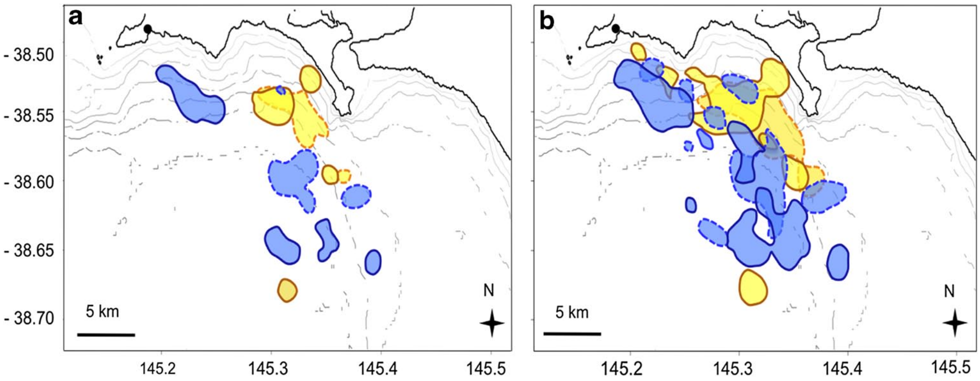

**Fig. 1** Distribution of little penguins in their foraging zone according to age and sex. Kernel density estimates zone of high prey encounter, (**a**) core (25 %) and (**b**) focal (50 %) areas of foraging in relation to middle-aged (*blue*) and old (*yellow*) age classes. The *dotted line* represents males and continuous line females. Seabed bathymetry at 10 m intervals is represented in *grey line*. *Black dot* marks the position of the colony

(Burnham and Anderson 2002; Symonds and Moussalli 2011). As no single model had an Akaike weight ($w_i$) above 0.90, we averaged models to calculate the relative importance of each explaining variable and potential interaction effect (Burnham and Anderson 2002; Symonds and Moussalli 2011). All models with a $\Delta$AICc $\leq 6$ were used in the model averaging with the package MuMIn in R (Burnham and Anderson 2002; Symonds and Moussalli 2011). For each variable, we summed the $w_i$ from each model containing this specific variable in order to get its relative importance (Burnham and Anderson 2002; Symonds and Moussalli 2011). Post hoc power analysis was conducted using G Power 3.1.9 (Faul et al. 2009) to compute statistical power on *t* tests between groups with non-significant results.

To quantify isotopic niche width and overlap, we used metrics based on standard ellipses, similar to standard deviation in univariate analysis to measure niche area and overlap among groups using the program SIBER in the *SIAR* package in R (Jackson et al. 2011). We compared four groups: the middle-aged females ($n = 7$) and males ($n = 3$), and the older females ($n = 4$) and males ($n = 9$). We calculated the Standard Ellipse Area corrected (SEAc) for small sample sizes (Jackson et al. 2011). While SEAc informs on the length of both axes, which are used to calculate the ellipse area, SEAc only gives one data point (ellipse) per group. For statistical comparison, we calculated Bayesian standard ellipse areas ($\text{SEA}_\text{B}$) using Markov chain Monte Carlo simulation with $10^4$ iterations for each group with 95 % credible limits among groups (Jackson et al. 2011). This method calculates the probability that the proportion of posterior samples of $\text{SEA}_\text{B}$ differed among groups, allowing a direct probabilistic interpretation of the differences in $\text{SEA}_\text{B}$ (sensu, Jackson et al. 2011).

## Results

Foraging locations and diving records were obtained from 26 individuals. Plasma stable isotope values were obtained from 23 of these individuals. All penguins headed southeast of Phillip Island (Fig. 1), travelling 20 ± 4 km (max. 30 km, in agreement with Collins et al. 1999) away from the colony and foraging in shallow waters along the continental shelf (55 ± 14 m). The penguins performed a total of 658 ± 27 dives per trip, of which 37 ± 1 % contained prey pursuits (Table 1).

### Spatial segregation

There was a clear segregation in prey pursuit distribution between middle-aged ($n = 11$) and old-aged ($n = 15$) penguins (Fig. 1). There was no overlap in the core area between groups, and a 3 % overlap in their focal area. Old penguins exploited the shallower waters closer to shore while middle-aged penguins went further offshore (Fig. 1; GLMM on the sea depth data: estimate $= -0.165$, SE $= 0.07$, $z = -2.3$, $p = 0.02$). Old males and females showed higher overlap in the core and focal foraging areas than middle-aged males and females (Table 2; Fig. 1).

There was a significant difference in bearings between the old and the middle-aged groups (GLM: estimate $= 0.0013$, SE $= 0.0003$, $t = 4.139$, $p < 0.001$), with middle-aged penguins heading on average towards SE (131 ± 3°) compared to ESE (120 ± 3°) for the old penguins. The major heading direction (bearing) taken by penguins was not affected by the interaction sex $*$ age (GLM: estimate $= 0.005$, SE $= 0.003$, $t = 1.681$, $p = 0.109$) or sex (GLM: estimate = -0.0008, SE $= 0.0004$, $t = -1.704$, $p = 0.105$).

Middle-aged penguins used a surface area 43 to 45 % larger than old penguins (focal area: 66 vs. 38 km$^2$ and

**Table 1** Average ± SE of all foraging parameters for each age class and sex

| | Middle-aged | | Old | |
|---|---|---|---|---|
| | Female ($n = 7$) | Male ($n = 4$) | Female ($n = 6$) | Male ($n = 9$) |
| Surface core foraging area (km$^2$) | 22.3 | 14.8 | 13.8 | 12.7 |
| Surface focal foraging area (km$^2$) | 57.3 | 42.3 | 40.5 | 29.8 |
| Diving parameter | | | | |
| Max distance (km) | 21 ± 2 | 20 ± 2 | 20 ± 2 | 19 ± 1 |
| Total distance (km) | 54 ± 3 | 54 ± 4 | 51 ± 2 | 52 ± 3 |
| Vertical distance (km) | 15 ± 2 | 17 ± 3 | 15 ± 2 | 18 ± 1 |
| Time underwater (%) | 34 ± 4 | 37 ± 6 | 36 ± 4 | 41 ± 2 |
| Number of dives | 613 ± 46 | 667 ± 73 | 634 ± 48 | 696 ± 59 |
| Hunting efficiency (%) | 36 ± 2 | 38 ± 3 | 33 ± 5 | 38 ± 3 |
| Horizontal segregation | | | | |
| Bearing (degrees) | 134.55 ± 3.71 | 125.26 ± 5.04 | 119.36 ± 6.43 | 120.50 ± 3.33 |
| Vertical segregation | | | | |
| Depth median (m) | 14.1 ± 2.0 | 14.5 ± 2.4 | 13.5 ± 1.3 | 14.5 ± 1.1 |
| Diet segregation | ($n_{DS} = 7$) | ($n_{DS} = 3$) | ($n_{DS} = 4$) | ($n_{DS} = 9$) |
| $\delta^{15}N$ | 15.50 ± 0.38 | 15.73 ± 0.33 | 15.22 ± 0.40 | 15.37 ± 0.25 |
| $\delta^{13}C$ | −20.44 ± 0.25 | −20.63 ± 0.06 | −20.79 ± 0.18 | −20.56 ± 0.13 |
| SEA$_C$(‰$^2$) | 2.16 | 0.39 | 1.17 | 1.01 |

Sample size ($n$) is in brackets. Foraging area was calculated using Kernel density for focal (50 %) and core (25 %) areas. All units are provided in brackets after each parameter. Sample size for the diet segregation ($n_{DS}$) is different than sample size for the other parameters

**Table 2** Area overlap (%) between males and females according to middle-aged and old-age classes distribution using Kernel density at (**a**) core (25 %) and (**b**) focal (50 %) of the foraging area, using the 'VI' method (see methods)

| | Middle-aged | | Old | |
|---|---|---|---|---|
| | Female ($n = 7$) | Male ($n = 4$) | Female ($n = 6$) | Male ($n = 9$) |
| (a) | | | | |
| Middle-aged | | | | |
| Female | – | 0 % | 0 % | 0 % |
| Male | | – | 0.4 % | 0.2 % |
| Old | | | | |
| Female | | | – | 6 % |
| Male | | | | – |
| (b) | | | | |
| Middle-aged | | | | |
| Female | – | 5 % | 1.5 % | 0 % |
| Male | | – | 5.6 % | 4.8 % |
| Old | | | | |
| Female | | | – | 18.4 % |
| Male | | | | – |

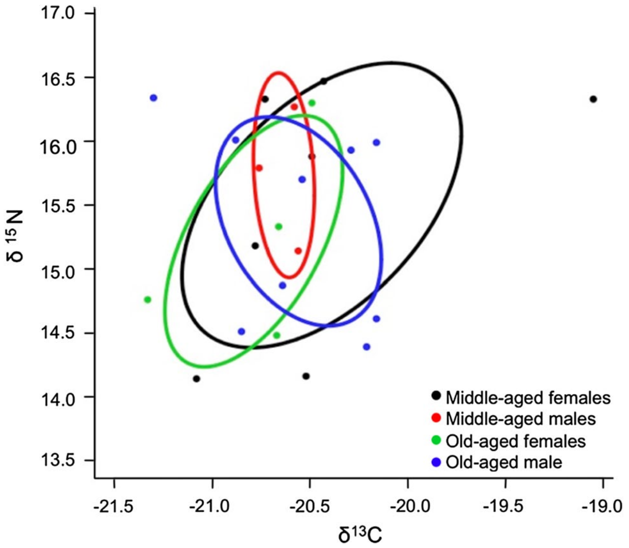

**Fig. 2** Niche occupancy of little penguins during guard stage at Phillip Island grouped by age and sex. The biplot depicting $\delta^{13}C$ and $\delta^{15}N$ isotope ratios. *Solid lines* represent standard ellipses and represent the isotopic niche width of 40 % of typical individuals within the group based on bivariate normal distribution following Jackson et al. (2011)

core area: 27 vs. 15 km$^2$, respectively). Females exploited a greater surface area than males in both the core and focal foraging areas, in both age classes (Table 1).

We did not find significant differences in the vertical segregation between age groups (Table 1). There was no effect of sex (GLMM: Estimate = −0.012, SE = 0.189, $z = -0.062$, $p = 0.95$), adult age (GLMM: Estimate = −0.003, SE = 0.012, $z = -0.225$, $p = 0.82$), or sex∗age (GLMM: Estimate = 0.008, SE = 0.016, $z = 0.497$, $p = 0.62$) on the maximum depth of foraging dives. For both groups, few dives with prey encounter were within 5 m of the seabed (2.15 % for the old and 1.17 % for the middle-aged birds).

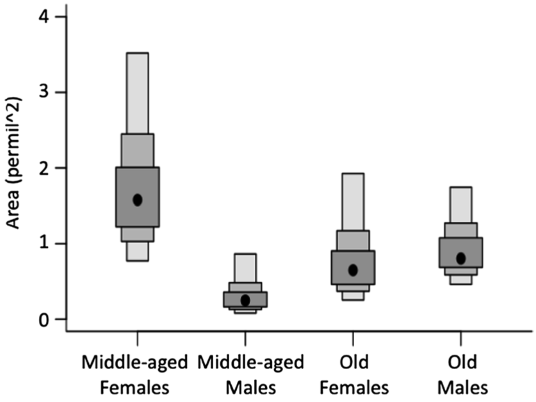

**Fig. 3** The credible interval for the estimated ellipse area estimate posterior distribution of little penguins during guard stage at Phillip Island grouped by age and sex. Each *bar* shows the range of Bayesian standard ellipse areas. *Black dots* represent the mode, and shaded boxes represent the 50, 75, and 95 % credible interval

### Dietary segregation

There was no significant difference in the stable isotope values of both $\delta^{13}C$ and $\delta^{15}N$ between sexes and age classes. The interaction sex ∗ age of the penguin was not significant for both $\delta^{13}C$ and $\delta^{15}N$ (All $p > 0.05$).

The different age/sex groups showed significant degrees of isotopic niche overlap (Fig. 2). For both age classes, the females had wider isotopic niche compared to the males (larger SEAc, Fig. 2; Table 1). Considering all age/sex groups, the middle-aged females displayed the largest isotopic niche (highest $SEA_c$), while the middle-aged males had the smallest one (Fig. 2; Table 1). From the Bayesian analysis ($SEA_B$), there was a high probability (more than 90 %) that middle-aged males had the smallest niche area (ellipse) (Fig. 3) between groups. In contrast, the middle-aged females had a low probability (less than 10 %) of having a smaller ellipse area compared to other groups (Fig. 3). The old-males exhibited a probability of 38 % of their niche area to be smaller than the old females.

### Foraging effort and efficiency

For all parameters of foraging effort and success, no models had an Akaike weight ($w_i$) exceeding 28 % (see Annexes 2 to 7). Moreover, for all parameters, the model with the highest Akaike weight corresponded to the null model (see Annexes 2 to 7). The sample size had a power to detect a medium effect size for the maximum distance and the percentage of time spent underwater, while for the other variables, our sample size had a low power (Annexe 8). Following Burnham and Anderson (2002), we included all models output from the MuMIn R package in the model averaging to avoid bias when low weight models are eliminated in the model selection.

No predictor variables showed a relative importance higher than 34 % in the model averaging (Table 3). The chick age was the predictor with the highest relative importance for the maximum distance (31 %). Parents travelled closer to the colony, covering smaller distance, as chicks grew older. The chick age had also the highest influence on the hunting efficiency (23 %), closely followed by the sex and body mass (both at 22 % of relative importance), while the adult age had the lowest relative importance on this parameter (Table 3). The adult age had the highest relative importance in explaining the variation in the total distance travelled (23 %). Diving behaviour parameters were primarily explained by adult sex followed by the chick age and date (Table 3). The body mass represented the lowest relative importance for most of the diving parameters (Table 3). The interaction between the age classes and sex of the adult had no influence on the different foraging parameters (Table 3).

## Discussion

Little penguins from Phillip Island spatially segregated while foraging offshore primarily by age and to a lesser extent by gender. This spatial segregation was not associated with a vertical (depth) or dietary segregation, but niche

**Table 3** Relative importance (in %) of the predictor variables and interaction

| | Adult age | Adult sex | Adult body mass | Chick age | Date | Adult age:sex |
|---|---|---|---|---|---|---|
| Maximum distance | 27 | 21 | 20 | 31 | 23 | 0 |
| Total distance travelled | 23 | 19 | 19 | 19 | 19 | 0 |
| Number of dives | 18 | 23 | 17 | 16 | 23 | 0 |
| % Underwater | 25 | 34 | 20 | 27 | 26 | 0 |
| Vertical distance | 18 | 29 | 17 | 25 | 18 | 0 |
| Hunting efficiency | 17 | 22 | 22 | 23 | 20 | 0 |

It was calculated as a sum of the Akaike weights over all of the models in which the parameter of interest appears. Adult age = Middle-aged and Old, Body mass = body mass of the adults, Adult age:sex = interaction between age class and sex of the adult, Date = date of the foraging trip size areas varied among sex and age classes, i.e. middle-aged females exhibited the larger isotopic niche area, while middle-aged males showed the smallest isotopic niche. Horizontal segregation has been observed in seabirds only occasionally at certain stages of the breeding cycle and at larger spatial scales than reported in our study. For example, black-browed (*Thalassarche melanophris*) and grey-headed albatrosses (*T. chrysostoma*) displayed large spatial scale segregation during long-range trips at the incubation stage, but not at small spatial scales when they foraged during the chick-rearing stage (Phillips et al. 2004).

The absence of dietary segregation and no differences in diving behaviour observed in our study could be attributed to high food availability within the foraging zone of our birds. Breeding success of little penguins during our study was well above average (using the breeding success scale given in Daniel et al. 2007) suggesting that prey were abundant (Chiaradia and Nisbet 2006). In years of low food availability or in late stages of chick rearing, differences in dietary segregation could become significant as observed in previous diet studies (Chiaradia et al. 2003, 2010, 2012).

Age-specific spatial segregation in foraging area has been reported in other species (Wunderle 1991; Sol et al. 2000; Daunt et al. 2007; Vanderhoff and Eason 2007). Older wandering albatross males segregated spatially and had lower foraging success than middle-aged males (Lecomte et al. 2010). The spatial segregation we observed in little penguins was similarly related to age of the adults. Indeed, the spatial segregation was always present, but more evident later in this study when chicks were older, coinciding with an increase in demand for energy required for growth and development (Chiaradia and Nisbet 2006) and yet limited by the maximum distance they can travel from the colony within a 1-day trip (Collins et al. 1999, this study).

Age-specific spatial segregation might be linked to the senescence process, as older seabirds would be physically and/or physiologically less fit than younger birds. Consequently, older seabirds may be unable to target high quality food resources and/or they could be excluded from the best feeding sites (Catry et al. 2006; Lecomte et al. 2010). For instance, senescence in wandering albatrosses was linked to differences in the foraging activity when older birds travelled a greater distance, but were less active at the sea surface followed by a decrease in reproductive investment (Lecomte et al. 2010). Older Cory's shearwaters (*Calonectris diomedea*) also reduced their daily activity compared to middle-aged birds foraging at sea. They spent more time on the water and had a smaller number of take-offs and landings during darkness, which might reflect a strategic regulation of investment in different activity (Catry et al. 2011) that can lead to spatial segregation. Yet, we found no effect of senescence on the little penguin's diving behaviour, measured by number of dives, percentage of time spent underwater, and the total vertical distance travelled, that could explain spatial segregation. We cannot rule out the possibility that the absence of strong effects of individual characteristics (e.g. age and sex) on diving behaviour could be due to the limitations in the number of birds tested (for financial and animal ethical limitations). Because of small sample sizes, there was power to detect a medium effect size only for the maximum distance and the time spent underwater. However, given the caveats of power analysis (Hoenig and Heisey 2001), our balanced sample size for each group and equal variance between groups have led us to accept the null hypothesis that there were no significant diving differences among the age groups.

Previous studies on little penguins have shown that middle-aged penguins have higher breeding success (Nisbet and Dann 2009), form non-random groups when crossing the beach (Daniel et al. 2007), and have higher diving efficiency (Zimmer et al. 2011a) than other age classes. In contrast to this trend, middle-aged penguins in our study did not benefit noticeably from segregating foraging zones, showing no increase in hunting efficiency and/or a decrease in foraging effort. Such a situation would only exist when prey availability is not a limiting factor (Shealer 2001). With increasing competition for resources, we would expect age-based differences in foraging ability to be enhanced. We can infer from our data that the quality and density of prey patches did not influence the observed age-specific segregation and in such conditions, individuals should be randomly spread, which was not the case in this study. Although segregation alone would benefit resource partitioning of a central forager with limited foraging zone like little penguins, our birds did not show any obvious 'energy-saving strategy' like albatrosses, where the senescent individuals try to maintain their body condition at the expense of the reproductive investment: here, the diving activity did not differ between middle-aged and old little penguins, although a reduction in physiological function may have taken place (see Elliott 2013). In other words, the segregation pattern we observed apparently depended only on an intrinsic trait of the individual, i.e. its age (cf. Schelling 1971).

Schelling's (1971) 'dynamic model of segregation' proposes that segregations can result when individuals prefer to associate with others that share similar characteristics i.e. their 'neighbours'. In the light of the 'dynamic model of segregation', we suggest that the pattern of segregation could result from either an attraction process, i.e. middle-aged birds preferring to forage with birds from the same age cohort, or avoid foraging with birds from a different age group. We believe the same age preference to be the most plausible explanation in the case of little penguins; individuals would naturally follow individuals with whom they share the same characteristics, as they can expect them to share similar needs and physiological constraints.

Cooperative foraging has been described in other penguin species (e.g. Takahashi et al. 2004; Copeland 2008), and it would seem likely that such cooperation develops among individuals that belong to the same cohort or at least closely-related ones. In little penguins, middle-aged birds, but no other age class form groups of 5–10 individuals just before leaving or arriving at the colony. In these middle-aged groups, individuals were neither nesting closely nor gender specific (Daniel et al. 2007). Our findings suggest that little penguins also retain this age-specific association while at sea. From our results, it seems clear that future studies trying to understand the mechanisms behind ecological segregation should take into account not only the spatial and temporal variability of the environment, but also the heterogeneity of the population studied as the characteristics of individuals and social interactions may play a vital role in explaining resource partitioning.

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