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Evaluating the relative importance of intrinsic and extrinsic factors on the foraging activity of top predators: a case study on female little penguins

I. Zimmer · Y. Ropert-Coudert · N. Poulin ·
A. Kato · A. Chiaradia

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Abstract A complex interaction of biotic and abiotic factors influences animal foraging activity. It is often difficult to understand which factors may affect animals' foraging and how it is affected. For instance, whereas the effect of sexual dimorphism on foraging activity has been reported in several species, little is known of the complex interactions between variables acting at a finer scale, e.g. the variability of body mass within a sex. Evaluating the importance of these finer scale factors is also essential to the understanding of foraging behaviour. We propose here a simple approach by applying principal component analysis (PCA) in a novel way to examine relationships between biotic and abiotic factors affecting foraging behaviour of top predators. We studied female little penguins (*Eudyptula minor*) of known age, carrying miniature accelerometers during the guard stage of breeding. Surprisingly, the body mass of the females did not influence any of the foraging parameters, but females foraging later in the breeding season dived shallower and more often, showing a strong correlation with laying date. Similarly, the diving effort of females was greater with increasing chick age within the same breeding stage. These results indicate that for female little penguin, the relationship between changes in prey availability and hunting effort can change at a fine scale, within a breeding stage. Therefore, any analysis of little penguin foraging behaviour during breeding should consider the timing in relation to the breeding season. We encourage researchers to develop the use of this PCA approach as it could help clarify the complexity of the underlying mechanisms determining foraging activity and we propose that it should be used as a first step of foraging behaviour analysis, before examining a particular relationship.

Introduction

Natural ecosystems are highly complex (Polis and Strong 1996), and understanding their structure and the dynamics of interactions between biotic and abiotic factors is critical for appreciating the persistence and stability of ecosystems (Dunne et al. 2005). Marine ecosystems are different from their terrestrial or freshwater counterparts due to (1) their openness, (2) the orders of magnitude in body size across species, and (3) the shortness of the trophic chains (Link 2002; Link et al. 2005). To evaluate ecosystem response to environmental change and its impact on overall ecosystem functioning, it is essential to disentangle the numerous factors (abiotic and biotic) that affect simultaneously marine organisms and to understand how key species respond to these factors.

Top predators can be used as ecological indicators to examine interactions in marine systems. Seabirds, which breed on land and forage at sea, are useful models to

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I. Zimmer, Y. Ropert-Coudert, A. Kato and A. Chiaradia contributed equally to the work.

I. Zimmer (✉) · Y. Ropert-Coudert · N. Poulin · A. Kato
Université de Strasbourg, IPHC,
23 rue Becquerel, 67087 Strasbourg, France
e-mail: izimmer76@gmail.com

I. Zimmer · Y. Ropert-Coudert · N. Poulin · A. Kato
CNRS, UMR7178, 67037 Strasbourg, France

A. Kato
National Institute of Polar Research, 10-3, Midoricho,
Tachikawa, Tokyo 190-8518, Japan

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

examine these interactions because they are generally long-lived, abundant and accessible on land (Piatt et al. 2007). Most seabirds live in a highly variable environment where their behavioural plasticity is a fundamental trait of their life history (e.g. Tremblay and Cherel 2003). Thus, seabird feeding adaptations reflect a diverse array of foraging strategies and tactics as well (Morrison et al. 1990). In addition, foraging behaviour differs between sexes (e.g. Bethge et al. 1997; Kato et al. 2000) and age groups (e.g. Rutz et al. 2006; Daunt et al. 2007; Limmer and Becker 2009), as well as between breeding stages (i.e. incubation, guard and post-guard, e.g. Williams and Rothery 1990) and years (e.g. Kato et al. 2003). However, little is known of the complex interactions among variables at a finer scale, e.g. the influence of body mass within a sex or the daily resource availability within a breeding stage. Evaluating the importance of fine scale factors may also help us understand seabird foraging behaviour.

Several methods have been developed to interpret foraging behaviour data generated by bio-loggers, including statistical clustering techniques and artificial neural networks (e.g. Schreer et al. 1998; Sakomoto et al. 2009). However, most are fairly complex and relate only to 2-D depth profiles (e.g. Fedak et al. 2001; Halsey et al. 2007). We propose a simple approach of interpreting bio-logging data, by applying principal component analysis (PCA) in a novel way to examine relationships between biotic and abiotic factors affecting foraging behaviour of little penguins. In most behavioural studies, PCA is used to reduce a high number of parameters into a few variables for further analysis, so as to simplify their interpretation (e.g. Lorentsen 1996; Elliott et al. 2008). To the best of our knowledge, PCA has not yet been used in foraging behaviour studies of top predators to investigate the relationship among the parameters themselves, despite of the statistical feasibility of this approach. Here, we describe the complex interaction of factors involved in the foraging activity of a penguin species by interpreting primary output from PCAs. Our model was the little penguin (*Eudyptula minor*), a piscivorous top predator of the waters around Australia and New Zealand and the smallest member of the Spheniscid species. Little penguins breed in burrows and are inshore central-place foragers that have a limited foraging zone (Chiaradia et al. 2007), which may change in relation to demands of different breeding stages (Collins et al. 1999). Breeding success in little penguins is a good proxy for food availability (Chiaradia and Nisbet 2006), which makes them good bio-indicators for changes in their environment (e.g. Chiaradia et al. 2003; Ropert-Coudert et al. 2009).

We eliminated the confounding effects of sex, breeding stage and inter-annual variability by examining only females foraging over a single breeding stage in a single, highly productive, breeding season. The analysis focused on four factors known to shape individually foraging activity, but we examined these at a finer scale than commonly done: (1) body mass differences within a sex (e.g. Kato et al. 2008), (2) daily changes in environmental conditions within a breeding stage (e.g. Chiaradia et al. 2007), (3) food demand of chicks as a function of the brood's age (e.g. Takahashi et al. 1999) and (4) adult age as a proxy for experience (e.g. Nisbet and Dann 2009). We investigated the relationship of these four factors with proximate foraging parameters that were selected to represent diving frequency and effort, prey availability and hunting effort.

Materials and methods

Fieldwork

This study was conducted on the little penguin breeding colony situated at the Penguin Parade on Phillip Island (38°31′S, 145°09′E), Victoria, Australia. Birds from this colony were injected with passive RFID transponder (Allflex, Australia) from the chick age, and the population has been monitored for more than 40 years (Dann 1992). From November to December 2005, we monitored foraging activity of 19 known age breeding females during chick guard with miniature accelerometers (M190-D2GT, Little Leonardo, Tokyo, Japan). Penguins in guard phase usually make 1-day trips regardless of year and breeding success (Chiaradia and Nisbet 2006).

Females were caught in their artificial nest boxes and weighed to the nearest 10 g using a spring balance. The accelerometer was attached onto the lower back of the penguin using waterproof tape (Wilson et al. 1997b). The attachment of the logger was completed in <5 min, and birds were returned to their nest boxes. After a single foraging trip, birds were recaptured, the logger and tape were removed, and the birds were weighed again before being released back to their nests. The birds' breeding success/failure was then monitored three times a week until chicks fledged.

The miniature accelerometer was cylindrical with a dome-shaped head (15 × 53 mm), had four-channel data loggers and weighed 17 g (Ropert-Coudert et al. 2006b for details). Depth was measured every second with an accuracy of ±1 m and a resolution of 0.05 m. Acceleration was measured along the longitudinal body axis (surging) and the dorsoventral axis (heaving) between 0 and ±30 $m.s^{-2}$ at 32 Hz. This sensor measured both dynamic acceleration (i.e. vibration) and static acceleration (i.e. gravity).

Dive analysis

The dive analysis was conducted on depth and acceleration data using IGOR Pro (Wavemetrics Inc., USA, 2008, Version

6.04). Data were corrected for surface drift and according to the resolution of the loggers, all dives >1 m were considered for analysis. The software analysed dives sequentially, writing a number of parameters for each dive into an output file. These were maximum dive depth (m); total dive and post-dive duration (s); descent, bottom and ascent duration (s); and the number and duration of dashes (s).

A dive started when a bird descended from the water surface and ended once the bird surfaced. The start and end of bottom phases were defined as the first and last time in a dive when the rate of change of depth became <0.25 m.s^{-1}. Flipper beats were apparent in the acceleration signals as an oscillating pattern being simultaneously present on both axes, with each propulsive stroke recorded on the heaving axis resulting in a forward acceleration recorded on the surging axis (Watanuki et al. 2006). The amplitude and frequency of each wing beat were analysed using the heaving acceleration signal (the most sensitive to undulation in the birds' body resulting from flipper beats). We found there was an upper amplitude threshold for normal diving wing beats (Ropert-Coudert et al. 2006b). Wing beat characteristics differed between individuals so that the threshold was adjusted for each bird. Prey pursuits (dash) were considered when the wing beat amplitude became greater than this threshold for more than three consecutive wing beats. The first 4 m of descent phases were excluded from dash detection because birds stroke their wings intensively to overcome buoyancy in the beginning of a dive.

Statistics

Principal component analysis (PCA) is a powerful tool to discriminate differences among the individuals under study when there are several variables (Jolliffe 1986). The main goal of the PCA is to explain the variability among individuals by gathering the variables that exhibit the same similarities or differences among the individuals investigated. A principal axis is a linear combination of variables built on the basis of the correlation coefficients among all available variables. Hence, instead of examining the variability or effects of each variable, PCA, in most studies, is used to reduce the variability in the data by explaining the grouping of the variables (axes or dimensions). The reduced number of variables can thus be used in linear or nonlinear models. However, PCA results themselves allow a direct interpretation by factor rotation. The first two dimensions generally explain most of the parameter variability and the parameter relations within these two dimensions then provide a trend of their similarities or differences. If the angle between parameters is ±180° their correlation equals −1, if this angle is ±90° they are independent from each other and a zero degree rotation (i.e. no rotation) is equal to a correlation of +1. This means that parameters are positively correlated when the angle between them is small (<45°) and negatively correlated when this angle is large (>135°). The closer an arrow reaches to the cycle the better it becomes explained by the first or second dimension.

In the present study, we were interested in specific variables (hereafter 'influencing factors') as a proxy for different key characteristics of foraging performance. Each influencing factor was considered independently in relation to all foraging parameters. These influencing factors were the adult body mass as a proxy for the physical characteristics (PCA1); the foraging date as an indicator of the environmental conditions (PCA2); chick age as an indicator of the food demand of chicks (PCA3) and adult age as proxy for their experience (PCA4). We examined how these factors could shape selected foraging parameters representing (1) the diving frequency (number of dives), (2) the diving effort (total time spent underwater, cf. Chiaradia et al. 2007; Takahashi et al. 2003, and mean bottom duration, cf. Boyd et al. 1995), (3) the prey distribution (median maximum dive depth, cf. Barrett and Furness 1990) and (4) the hunting effort (percentage of prey encounter dives and total time of prey pursuit, e.g. Ropert-Coudert et al. 2006b). The PCA only considers one single value per individual and per foraging parameter or influencing factor, which was always calculated for one single guard foraging trip. Median values were used for the maximum dive depth since diving data are rarely normally distributed. Maximum dive depth influences most dive parameters (Wilson et al. 1997a; Cherel et al. 1999). To take depth into account, we calculated least square means for the parameter bottom duration from a general linear model using JMP 8 (SAS Institute Inc.), which included maximum dive depth as a covariate.

PCAs were conducted with R software (R Development Core Team 2009) using the FactoMineR package (1.10, Lê et al. 2008). The number of dimensions selected for analysis was reduced to three nonredundant axes following the Kaiser criteria, i.e. only considering axes with an eigenvalue >1. We selected the first two dimensions with the highest loadings (axis 1 and 2) for presentation and interpretation of data and these axes together always explained >59% of the variability. The first two dimensions of PCA results are presented by correlation circles, so-called variable factor maps (Fig. 1). In addition, to assist the interpretation of the data, the table includes the first three PCA component loadings of influencing factors and foraging parameters for the four performed PCAs. The data used in the PCA are presented in Appendix.

Results

Foraging parameters showed a similar pattern in PCAs 1–4 in regard to dimensions one and two (Fig. 1; Table 1). In all

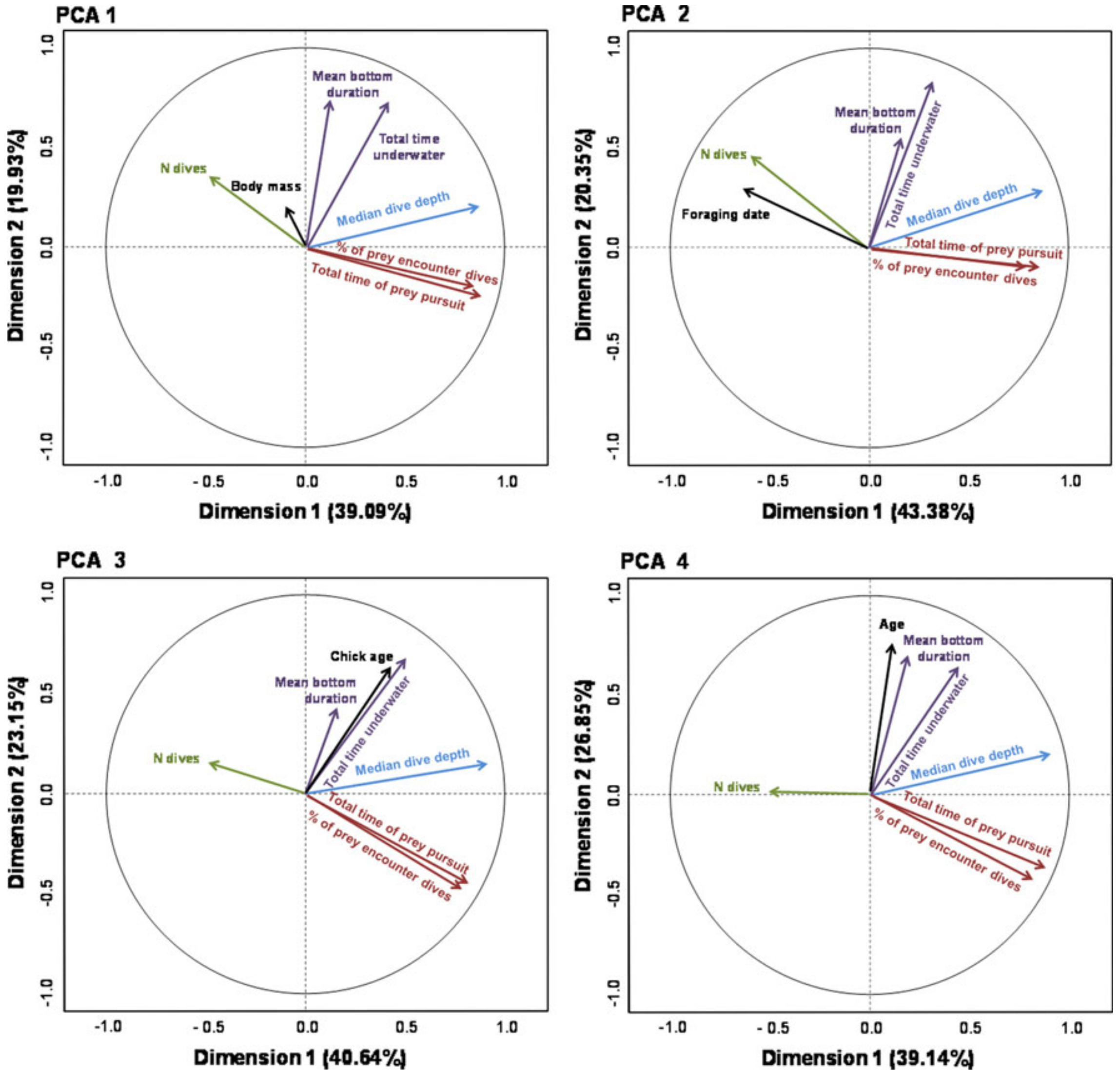

Fig. 1 Four variable factor maps (PCA 1–4) presented by their first two component loadings. All PCA present the same selection of foraging parameters that were chosen to represent (1) the diving frequency (number of dives), (2) the diving effort (total time spent underwater and mean bottom duration), (3) the prey distribution (median maximum dive depth) and (4) the hunting effort (percentage of prey encounter dives and the total time of prey pursuit). Each PCA was performed with one of the following four factors, which were expected to affect foraging behaviour: body mass as a proxy for the physical characteristics (*PCA1*), the date of foraging as an indicator of the environmental conditions (*PCA2*), the chicks' age as an indicator for chick food demand (*PCA3*) and adult age as a proxy for penguins' experience (*PCA4*)

PCAs, an increase in median dive depth and hunting effort was followed by a decrease in the number of dives over a foraging trip (Fig. 1). Also, if penguins spent more time underwater, the bottom duration of dives increased as well.

Female body mass was normally distributed and not strongly related to any of the foraging parameters (Table 1; Fig. 1; see also Appendix). The PCA1 best represented this factor with the third dimension, which only explained 16.2% of the total variation (Table 1). No other foraging parameter became well expressed by this third dimension, and body mass was only poorly explained by dimension one and two (Table 1). In other words, there was no influence of 'adult body mass' on any of the foraging parameters.

Penguin foraging behaviour was strongly related to the foraging date. Penguins foraging later in the breeding season dived shallower and more often (PCA2, Table 1; Fig. 1). At the same time, the hunting effort decreased over a foraging trip.

With increasing age of chicks, females spent more time underwater during a guard trip and the bottom dive duration of dives increased (PCA3, Table 1; Fig. 1). This strong relationship indicates an increased diving effort. Despite the lack of a significant correlation, PCA3

Table 1 Component loadings of four principal component analyses (PCA) of foraging parameters of female little penguins from Phillip Island during the guard period in 2005 that collectively explained 78.5% (PCA 1), 82.9% (PCA 2), 82.1% (PCA 3) and 83.3% (PCA 4) of the total variance

	Dim. 1	Dim. 2	Dim. 3
PCA 1 (%)	39.1	19.9	16.2
Influencing factor			
Body mass	−0.09	0.20	**0.90**
Foraging parameters			
N dives	**−0.50**	0.36	0.05
Median depth	**0.89**	0.21	−0.12
Total time underwater	0.41	**0.73**	−0.36
Mean bottom duration	0.12	**0.74**	0.23
% of prey encounter dives	**0.85**	−0.19	0.33
Total time of prey pursuit	**0.89**	−0.25	0.07
PCA 2 (%)	43.4	20.4	17.1
Influencing factor			
Foraging date	**−0.64**	0.30	0.52
Foraging parameters			
N dives	**−0.59**	0.47	0.43
Median depth	**0.87**	0.28	0.02
Total time underwater	0.32	**0.85**	0.06
Mean bottom duration	0.16	0.54	**−0.65**
% of prey encounter dives	**0.81**	−0.08	0.36
Total time of prey pursuit	**0.85**	−0.09	0.42
PCA 3 (%)	40.6	23.2	15.4
Influencing factor			
Chick age	0.43	**0.66**	−0.5
Foraging parameters			
N dives	−0.51	0.17	**0.64**
Median depth	**0.92**	0.16	−0.01
Total time underwater	0.50	**0.70**	0.29
Mean bottom duration	0.15	0.45	**0.49**
% of prey encounter dives	**0.78**	−0.48	0.26
Total time of prey pursuit	**0.82**	−0.46	0.16
PCA 4 (%)	39.1	25.4	16.0
Influencing factor			
Adult age	0.10	**0.82**	−0.38
Foraging parameters			
N dives	−0.5	−0.04	**0.81**
Median depth	**0.90**	0.23	0.02
Total time underwater	0.43	**0.61**	0.52
Mean bottom duration	0.15	**0.61**	0.17
% of prey encounter dives	**0.83**	−0.42	0.14
Total time of prey pursuit	**0.88**	−0.35	0.07

PCA 1–4 differ with respect to one factor that was expected to influence the foraging parameters: (1) body mass (PCA1), (2) foraging date (PCA2), (3) chick age (PCA3) and (4) adult age (PCA4)

Parameters accounting for most of the variation in each principal component are shown in bold

indicated that females may increase their hunting effort with increasing age of their chicks.

Older females had longer mean bottom dive durations and spent more time underwater (PCA4, Table 1; Fig. 1), but age was not closely related to any other foraging parameters.

Discussion

Our study aimed at evaluating interactions between intrinsic and extrinsic factors and foraging parameters of a marine top predator as a first step before examining each foraging parameter independently in the analysis of foraging behaviour data. We suggest that this first step is crucial in indicating those relationships that are important and should be considered in subsequent foraging behaviour analysis.

Our results highlighted the influence of environmental conditions (foraging date), food demand of growing chicks (chick age) and adult experience (adult age) on several foraging parameters. Body mass did not show a relationship on the chosen foraging parameters, as demonstrated by its weak representation in the first two dimensions of the PCA. Body size/mass is usually seen to influence foraging parameters (Beck et al. 2003; Kato et al. 2008). However, body mass is also known to be dependent on sex in little penguins (Dann et al. 1995) and since our analyses were only on females, we conclude that individual variability in body mass within sex had a limited influence on the chosen foraging parameters in this study.

Environmental conditions

Diving behaviour changed in relation to foraging date, suggesting variability in food availability and/or distribution during the breeding season. With progressing season, penguins dived shallower and more often, but at the same time penguins decreased their hunting effort. There may be several possible explanations for this. Individuals may adjust their diving behaviour to include more shallow dives due to changes in the prey distribution or due to the availability of a different prey in shallow waters (e.g. Croxall et al. 1988; Kato et al. 2003; Wilson et al. 1993). A simultaneous decrease in hunting efficiency could be explained by a reduction in prey patch density (Ropert-Coudert et al. 2009) or changes in the pursuit pattern of foraging penguins according to the prey type, i.e. targeting less mobile prey (e.g. Ropert-Coudert et al. 2006a). Reproduction takes place at the most favourable time of the year, and the onset of breeding is often dependent upon food availability (i.e. Meijer and Drent 1999), with early breeders generally being more successful than late breeders (Nisbet and Dann 2009). Due to decreasing food availability later in the season (Chiaradia and Nisbet 2006), late breeders would have to alter their foraging strategies in response to prey changes. The guard stage is a crucial phase of the breeding cycle for seabirds, as parents have to frequently return to their nest to feed their offspring in order to be successful (Takahashi et al. 2003). In breeding little penguins, this constraint is even further aggravated since birds rely on food supply directly in the vicinity of the colony and may not be able to undergo long trips in order to target more profitable distant prey patches like they can do during the incubation period (Kato et al. 2008).

Food demand of growing chicks

We suggest that the penguins increased their diving effort in order to encounter more prey as the chicks' food demands increased with age, since meal sizes increase with chick age during the guard phase (Chiaradia and Nisbet 2006). This confirms a trend among central-place seabirds that face an increase in chicks' demand for food over the season, which in turn leads to greater diving effort (e.g. Williams and Rothery 1990; Bethge et al. 1997). Surprisingly, the hunting effort did not increase with chick age. Some species do not adjust food delivery to chick demand (e.g. Leach's storm petrels *Oceanodroma leucorhoa*, Takahashi et al. 1999), but it has been demonstrated in several instances that chicks can modulate parental provisioning effort through begging behaviour (Hussell 1988; Kitaysky et al. 2000). Our results suggest that the efficiency of prey capture by adult little penguins was independent from chick demands and solely depended on prey availability as 2005 was a year of high breeding success, an index of good resource availability (Chiaradia and Nisbet 2006). Although begging behaviour is not well studied in little penguins (e.g. Nakagawa et al. 2001), we suspect that adults were probably able to supply their chick with enough food to limit the influence of chick begging on their provisioning activity.

Adult age

Our results show an increase in diving effort with adult age as influencing factor, but interestingly no strong relationship between age and hunting effort. Improvement in the hunting skills of a predator would play an important role in explaining foraging success (i.e. Rutz et al. 2006). In long-lived animals, reproductive performance improves with age, at least during the early years of breeding (e.g. Martin 1995; Ezard et al. 2007). Age-related breeding experience has been extensively studied in birds due to their longevity (e.g. Martin 1995; Holmes et al. 2001). For example, the dependence of breeding performance on parental age in little penguins is curvilinear, peaking about at 8 years of age (Nisbet and Dann 2009). Similarly, chick provisioning has been shown to improve with parental experience in other seabirds (e.g. in common terns *Sterna hirundo*, Limmer and Becker 2009). Experience is an important indicator of individual quality and as such, the improvement in breeding performance and success is expected to reflect the development and improvement of foraging skills (e.g. Rutz et al. 2006; Daunt et al. 2007). Several authors (e.g. Sydeman et al. 1991; Barbraud and Weimerskirch 2005; Lescroël et al. 2009) have predicted an interaction between age and extrinsic conditions on foraging performance, with differences more apparent when feeding conditions are poor. Coincidentally, our study year corresponded to a year of apparently high prey availability (cf. Chiaradia and Nisbet 2006; Ropert-Coudert et al. 2009). This may explain why we did not find a strong relationship with hunting effort: when food supply is not limited, differences in foraging performance birds of different ages/experience are not apparent, and hunting effort is then not related to age.

Predator foraging studies are often based on discrete foraging trip deployments that represent a snapshot of the foraging behaviour at a given breeding stage. Our novel use of PCA suggests caution should be exercised when comparing diving performance of animals monitored on different dates, even within the same breeding stage, since changes in environmental conditions as the season progresses may be a confounding factor when examining foraging parameters. We also showed that the offspring's age can be a significant factor and so we suggest including this factor into statistical models when examining foraging parameters.

We encourage researchers to develop the use of this approach to identify, although not quantify, the relationships between influencing factors and foraging parameters. Our results indicate that, at least for little penguin females, the relationship between changes in prey availability and hunting effort can change at a fine scale within a breeding stage. Therefore, analysis of foraging behaviour should take these factors into consideration, without ignoring the potential influence of adult age on diving effort, particularly during years of poor resource availability. We believe the way we used PCA could help clarify the complexity of the underlying mechanisms determining foraging activity, and we propose that it should be used as a first step of foraging behaviour analysis, before examining a particular relationship.

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Appendix

See Table 2.

Table 2 Summary of the foraging parameters used in the PCA and life history traits of little penguins

Bird ID	Age (yr)	Body mass (g)	Foraging date	Chick age (d)	*N* dives	Median depth (m)	Total time underwater (s)	Mean bottom duration (s)	% of prey encounter dives	Total time of prey pursuit
G3021F	3	1,060	26/11/2005	3	728	2.88	16,114	8.70	12.50	355.06
G3058F	3	1,220	29/11/2005	2	1,957	3.17	17,420	8.56	27.80	666.84
G4021F	3	970	17/12/2005	4	2,149	3.22	22,825	7.20	9.40	353.84
G3034F	4	1,110	24/11/2005	3	745	6.25	17,793	5.00	14.63	789.66
G3052F	4	1,130	04/12/2005	4	926	2.98	18,066	9.24	9.72	418.78
G3113F	4	1,020	23/11/2005	9	565	10.94	16,205	8.85	30.80	932.41
G8077F	4	1,000	11/12/2005	NA	1,067	5.23	19,395	9.19	23.62	667.69
G3087F	5	1,050	15/11/2005	4	574	20.95	23,606	7.75	46.52	1,797.91
G3092F	5	870	21/11/2005	5	542	3.03	9,967	4.99	15.68	655.94
G8046F	5	970	12/12/2005	NA	1,380	3.13	25,955	7.67	22.61	1,160.34
G3124F	6	1,050	18/11/2005	NA	1,328	3.42	21,017	8.46	11.75	332.81
G8011F	6	1,020	09/12/2005	2	1,906	1.91	14,062	8.01	6.82	284.88
G3004F	7	1,070	03/12/2005	3	1,069	2.39	11,934	6.19	17.59	842.69
G3007F	10	1,060	27/11/2005	4	710	2.95	13,853	9.89	16.34	403.03
G3105F	11	960	18/11/2005	7	1,102	6.25	26,062	9.26	9.89	618.81
G3062F	13	1,020	15/11/2005	NA	757	15.63	26,145	11.02	18.23	802.00
G3076F	13	1,050	22/11/2005	5	665	4.54	17,755	9.20	13.23	687.72
G3082F	14	1,150	10/12/2005	4	1,004	3.37	18,925	7.76	11.65	396.88
G3116F	14	1,020	09/12/2005	14	944	13.62	28,702	7.17	10.59	412.34

NA indicates that the chick age was not known

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