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Maria Gomes Ribeiro Teixeira Pinto

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Dissertação de mestrado orientada por

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Resumo

Muito pouco se sabe sobre a ecologia reprodutora da ave marinha Alma-Negra (*Bulweria bulwerii*), principalmente sobre o seu comportamento e sobre os fatores e mecanismos responsáveis pelo seu sucesso reprodutor. Neste estudo foram investigados dois aspectos da ecologia reprodutora das Almas-Negras da colónia da Ilha Selvagem Grande, pertencente ao arquipélago da Madeira: a influência do ciclo lunar na alimentação das crias e o comportamento de permanência dos progenitores no ninho durante os primeiros dias após a eclosão das crias – comportamento de guarda do ninho. A colónia da Ilha Selvagem Grande é um dos principais núcleos reprodutores desta espécie no Atlântico. A compreensão dos fatores que podem influenciar o seu sucesso reprodutor e o seu comportamento irá permitir, para além de obtenção de nova informação sobre a ecologia destes predadores de topo, determinar como estas aves marinhas se adaptam a diferentes condições, através da comparação com outras colónias e espécies.

O trabalho de campo na Selvagem Grande foi realizado durante a época de reprodução da Alma-Negra, em 2009 e 2012. Estes ninhos foram monitorizados diariamente, sempre à mesma hora e pela mesma ordem desde o início do período de amostragem até os ovos ou crias morrerem ou desaparecerem. Após eclodirem, começando no primeiro dia em que foram encontradas no ninho sem progenitores, as crias foram pesadas diariamente e a asa foi medida com uma régua. Adicionalmente, e apenas no ano de 2012, os dias de guarda ao ninho pelos progenitores foram contados e registados.

Para investigar a influência do ciclo lunar na variação diária do peso das crias, utilizada como uma medida aproximada da alimentação das crias, utilizaram-se modelos lineares mistos e ANOVAs com medidas repetidas. Os resultados mostraram que o ciclo lunar (medido como a proporção de lua visível à meia noite) influenciou negativamente a variação diária de peso das crias, mas apenas no período em que estas tinham em média entre 30 e 60 dias de idade, tanto em 2009 (χ^2= 6.57, P<0.05) como em 2012 (χ^2= 13.91, P<0.001). Adicionalmente, quando comparadas as variações diárias de peso das crias apenas entre o período de lua cheia e o período de lua nova, encontrou-se uma diferença significativa entre ambas tanto em 2009 como em 2012. Esta diferença foi encontrada tanto em crias que nasceram antes do pico de eclosão (em 2009, F=6.44, p<0.05 e em 2012

F=25.45, p<0.001), como em crias que nasceram depois do pico de eclosão (em 2009, F=38.68, p<0.001 e em 2012 F=10.91, p<0.01). Estes resultados mostram uma clara influência da fase lunar na alimentação das crias - em noites em que há mais luar as crias comem menos. Esta influência já foi verificada em várias colónias de aves marinhas. No caso das Almas-Negras, poder-se-á dever principalmente a dois fatores: 1) ao facto dos progenitores poderem vir menos vezes à colónia em noites com mais luminosidade, para evitar serem detetados por predadores (neste caso, pelas Gaivotas-de-patas-amarelas *Larus michahellis atlantis*, que também se reproduzem na Selvagem Grande); e/ou 2) ao facto da taxa de captura de alimentos pelos progenitores ser influenciada pela lua, uma vez que predam espécies de zooplâncton mesopelágico que fazem migrações verticais diárias, as quais não são tão pronunciadas em noites de luar.

Na segunda parte do trabalho foi estudado o comportamento de guarda de ninho dos progenitores de Alma-negra. Sabe-se que as aves marinhas permanecem no ninho para auxiliar as crias até estas atingirem a homeotermia; no entanto, alguns estudos sugerem que o comportamento de guarda do ninho poderá ter mais alguma função, uma vez que em algumas espécies os progenitores permanecem no ninho até depois das crias atingirem este estado. Algumas hipóteses já foram sugeridas para explicar este comportamento. As hipóteses que pudemos analisar neste estudo foram a *hipótese da sincronia* e a *hipótese de assistência no crescimento*. A *hipótese da sincronia* afirma que as crias beneficiam se eclodirem ao mesmo tempo, pois isto diminui a probabilidade de cada indivíduo ser predado. Isto sugere que em casos onde existe predação se verificará um declínio do tempo de guarda de ninho ao longo do período de eclosão - os progenitores permanecem mais tempo no ninho se as crias eclodirem mais cedo, sendo que assim quando as deixarem no ninho sozinhas já mais crias terão eclodido, diminuindo a probabilidade de cada cria ser predada, devido a um efeito de diluição. A *hipótese de assistência no crescimento* prevê que crias guardadas por mais tempo atinjam maior massa nos primeiros dias de vida do que aquelas guardadas menos tempo. Esta hipótese apoia-se nos pressupostos, de que ao serem guardadas mais tempo as crias gastam menos energia noutras funções básicas (nomeadamente termorregulação), permitindo uma maior taxa de crescimento, e também de que ao estarem constantemente na presença de um progenitor recebem refeições mais pequenas mas mais frequentes, ideal para quando têm poucos dias de idade com um estômago pequeno e taxa de digestão elevada. Para estudar estas hipóteses e ajudar na compreensão da origem do comportamento de guarda do ninho, no presente estudo investigou-se a relação entre a duração de guarda do ninho com: a massa das crias cinco dias após a eclosão (variável denominada Massa 5); a data de eclosão das crias; e a sobrevivência das crias. Adicionalmente investigou-se a relação entre a Massa 5 e a data de eclosão das crias e a fase da lua.

A duração de guarda do ninho variou entre 0 e 4 dias (média ± SD: 1.56 ± 0.89, n=57). A duração de guarda ao ninho não influenciou a Massa 5, o que sugere que este comportamento não tem o papel de auxiliar as crias no seu crescimento durante os primeiros dias de vida, rejeitando-se a *hipótese de assistência no crescimento*. Este resultado era expectável pois é pouco provável que num clima quente, como aquele encontrado na Selvagem Grande, a energia poupada pela cria devido à presença de um progenitor no ninho contrabalance o facto de apenas um progenitor estar em busca de alimento.

Foi encontrado um declínio sazonal na duração de guarda de ninho (S=27207.14, r=-0.31, p <0.05), ou seja, quanto mais tarde as crias eclodiram, menos tempo os progenitores se mantiveram no ninho após a eclosão. Estes resultados suportam a *hipótese da sincronia*, indicando que este comportamento poderá ser utilizado como uma estratégia anti predatória pelos progenitores de Almas-Negras

Foi também encontrada uma correlação entre o dia de nascimento das crias e a Massa 5 (t=3.07, df=48, r=0.41, p<0.01). Este resultado poderá ser também devido à fase lunar (devido aos mesmo motivos discutidos na primeira parte do trabalho), uma vez que a Massa 5 de crias nascidas em período de lua nova foi superior à das crias nascidas em período de lua cheia (t=-3.41, df=21.09, p<0.01). No entanto, uma vez que o período de eclosões foi apenas de 16 dias, este acontecimento poderá ser devido a outros factores que coincidiram por acaso com diferentes fases lunares. Para aprofundar a compreensão deste comportamento será necessário investiga-lo em anos diferentes, em colónias diferentes e em condições distintas, para perceber concretamente que fatores poderão influenciar o tempo de guarda de ninho e qual a sua finalidade.

Este estudo permitiu concluir que o ciclo lunar influencia a alimentação das crias de Almas-negras da colónia das Ilhas Selvagens e que o comportamento de guarda de ninho poderá ter outra função que não apenas a de auxiliar a cria na manutenção da temperatura até atingir a homeotermia.

Abstract

The breeding ecology of the seabird Bulwer's Petrel (*Bulweria bulwerii*) has been poorly studied, as well as factors and mechanisms underlying their breeding success. In this study two aspects of the reproductive ecology of the Bulwer's Petrel colony of the Selvagem Grande Island, Madeiran Archipelago, were studied. This is one of the most important colonies of this species in the Atlantic. I aimed to understand whether the lunar cycle has an influence on chicks provisioning and to understand the importance of brood guarding behaviour for further understanding of the mechanisms underlying and controlling it. Daily chicks weight variation was used as a proxy of chick provisioning.

Moon phase (percentage of the visible disk at midnight) negatively influenced the daily weight variation of chicks in both years, but only at the later stages of their development (30 to 60 days olds, in average). Also, when comparing the variation of the chicks weight between only new moon and full moon periods, a significant difference was found, for both years. These results show a clear influence of the lunar cycle in Bulwer's Petrel chicks provisioning at least in one phase of their growth. This influence is probably due to less nest attendance by parents on moonlight nights to avoid predation, and/or to a reduction on prey availability around full moon, given that they prey upon zooplankton that performs daily vertical migrations, which are negatively influenced by moonlight.

Brood-guarding duration had no effect on chicks mass at their fifth day after hatching (Mass5) or on chick survival; however a seasonal decline was found between hatching date of the chicks and brood guarding duration. Additionally, a correlation was also found between hatching date and Mass5. Mass5 of chicks born during new moon period was significantly different from Mass5 of chicks born outside this period. A seasonal decline in chicks brood-guarding duration supports that this might be an anti-predatory strategy to decrease chicks probability of being predated. Also, the lunar cycle seems to influence chick provisioning in the first days of their life during brood-guarding.

Keywords: Bulwer's Petrel, Chick provisioning, Brood guarding, Selvagem Grande

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I. Introduction

Background

Seabirds are major consumers in marine food webs. They are top consumers in pelagic marine systems, and are greatly influenced by oceanographic conditions and by the distribution of their prey (Diamond and Devlin 2003, Weimerskirsh 2007).

Procellariiformes order is among the few exclusively marine bird orders, and individuals are highly adapted to a pelagic lifestyle (Hoyo et al. 1992). They are characterized for having a straight bill with a hooked tip, and tubular external nostrils which grants them a remarkable sense of smell that they seem to use for navigating throughout the oceans, individual and nest site recognition, and foraging (Nevitt 2008). Besides these features they possess other morphological and behavioural adaptations that allow them to spend most of their life at sea, returning to land only for a few months a year for mating, breeding and chick rearing. Along with other Procellariiformes, members of the Procellariidae family generally breed in large colonies, strategically placed near the sea, avoiding areas where predators abound (Hoyo et al. 1992).

Having to cope with highly variable food availability, pelagic seabirds have adopted life history strategies to adapt to this situation, as delayed maturity, long lifespan, low annual reproductive output, and slow chick growth (Tveraa et al. 1998, Ricklefs 1990). Nevertheless, seabird reproduction period is a really demanding time, where parents face a trade-off between their survival and the one of their chicks (Burke and Montevecchi 2009) - they have to balance provisioning their chick with their own condition and risk of being predated.

Couples from the Procellariidae family lay only one egg per year (Ricklefs 1990), and after hatching they go out to the sea to find food. As a rule, only Fulmar-Petrels visit their colonies by day. Even though some species - the Black-winged Petrel (*Pterodroma nigripennis*), the Kermadec Petrel (*Pterodroma neglecta*), the Herald Petrel (*Pterodroma arminjoniana*) and the Cory's Shearwater (*Calonectris diomedea*) - may also visit their breeding colonies during the day, this only happens in rare occasions when colonies are located in islands free of avian predators (Tennyson and Taylor 1990, Hutton and Priddel 2002); in most cases, parents return to their breeding colonies only at night.

The need to return to the colony to feed their chicks limits the available foraging areas, while also increase their vulnerability to predation. These birds have developed a wide variety of strategies to maximize their survival probability without discarding the survival of their chicks. For instance, there seems to be a high flexibility in foraging strategies among different and within species, allowing parents to respond to variability of prey availability and environmental conditions (Waugh et al. 2000): many Procellariiformes have a dual-foraging strategy, alternating repeated short trips with long trips to more productive and with higher prey availability waters (Weimerskirch et al. 2003), while others seem to rely solely on one of the both types of trips (Weimerskirch 1998). Short trips allow a higher provisioning rate of the chicks, and long trips allow the maintenance of the mass condition of the adults above a certain threshold reducing their own survival costs (Chaurand and Weimerskirch 1994). This situation highlights the trade-off between parents own survival and chick provisioning. Variability within the same species indicates that the strategy adopted might be highly influenced by environmental conditions, prey availability and predatory pressure (Magalhães et al. 2008).

Bulwer's Petrel (*Bulweria bulwerii*)

The Bulwer's Petrel *Bulweria bulwerii* (Jardine & Selby, 1828) is a black coloured petrel that belongs to the Procellariidae family. It has long narrow wings and a long pointy tail (Figure 1), its length ranges from 25 to 29 cm, its wingspan from 67 to 73 cm (Svensson et al. 2009) and its weight from 78 to 130 g (Hoyo et al. 1992).

This pan-tropical species has breeding populations in both the Atlantic and Pacific oceans (Zonfrillo 1985). In the Atlantic its distribution is restricted to the Macaronesian archipelagos of Madeira, Azores and Canary and, in smaller numbers, in Cape Verde archipelago (Equipa Atlas 2008). In the Pacific Ocean it can be found from Eastern China and Bonin islands to Hawaii, Phoenix and Marquesas islands (Hoyo et al. 1992).

Like all other Procellariiformes, the Bulwer Petrel is a pelagic species that spends most of its time far from land, except during the reproduction period, which can range from April to September (Bartle et al. 1993, Ramos and Trujillo 2004). This bird nests in large colonies located on isolated islands (Bruun 1978), among boulders or in cliff cavities, usually near the sea (Ramos and Trujillo 2004, BirdLife International 2013). In the Atlantic, adults arrive at their colonies in early May, lay in June and eggs hatch around mid-July, chicks and parents then leave the colony in late September (Monteiro et al. 1996). Each couple lays only one egg per season, and during incubation there is always at least one parent at the nest. After the hatching and a short period of brooding, both parents fly out to the sea in pursuit of food for the chick (Hoyo et al. 1992), who is then fed during the night. Individuals of this species normally do not flock and tend to forage alone, though small groups can be seen when feeding at sea (Svensson et al. 2009). The diet of this species is poorly known, but recent studies indicate that it is based on small cephalopods and mesopelagic fish (Spear et al. 2007, Neves et al. 2011, Carvalho 2012).

Figure 1 - Bulwer's Petrel: adult (A) and chick (B)

Globally, the species is categorized as “least concern” (BirdLife International 2013). The population global estimation was between 500.000 and 1.000.000 of individuals (Brooke 2004). However, both in the Azores archipelago and Spain it is categorized as “endangered”, due to the small distribution range, reduced population numbers (Monteiro et al. 1999, Ramos and Trujillo 2004, Almeida et al. 2008) and a significant decrease of breeding sites probably due to the increase of touristic activities (Ramos and Trujillo 2004) and of the number of introduced predators such as cats and rats (Luzardo et al. 2008). The colonies located in the Madeira Archipelago - Desertas and Selvagens - have not been quantified yet, but are considered to hold the main core of Bulwer’s Petrel population in the Atlantic Ocean

(Equipa Atlas 2008). Their distribution during the non-breeding periods is almost unknown; however it appears that they can travel far south to winter in southeast of the Brazilian coast (Monteiro et al. 1996, Zino et al. 2012).

In this study two components of the breeding ecology of the Bulwer's Petrel colony from Selvagem Grande Island were investigated: brooding behaviour and the influence of the lunar cycle in chick provisioning.

While the breeding chronology of the Bulwer's Petrel is relatively well known (Whittow 1994, Nunes and Vicente 1998), its breeding biology and behaviour on the Pacific and Atlantic colonies is far from understood. However some advances have been made in understanding the breeding biology in two major colonies of the Atlantic, namely in Desertas Islands (Nunes and Vicente 1998, Nunes 2000) and in the Azorean Archipelago (Monteiro et al. 1996). However, still very little is known of the factors regulating and influencing their breeding success and behaviour.

Understanding the breeding ecology of the Bulwer's Petrel in single colonies, subjected to different conditions, will allow a better comprehension of how they adjust and adapt to different environmental and biological factors, during this critical time in their survival. Therefore, information about how the lunar cycle affects breeders from one of the most important Atlantic colonies, as is the one from Selvagem Grande Island, will take us one step closer in understanding the importance of environmental variables in this species reproductive success and how they might influence populations of seabirds in general. Brood-guarding, considered to be a continual attendance at the nest by parents after hatching, is widespread among seabirds, however very few is known about its role in chick survival and the mechanisms and factors underlying and regulating it; furthermore, no research has ever been made regarding this behaviour on the Bulwer's Petrel. Investigating brooding behaviour of this species will offer further information for determining its importance and influence on chick survival and consequently on reproductive success in both the Bulwer's Petrel and seabird community.

II. Does the lunar cycle affect chick provisioning in Bulwer's Petrels?

Introduction

Lunar cycle has been shown to be an important factor in the life of several animals, mostly due to the effect of moonlight in survival and foraging success through changes in predation risk and prey availability (Skutelsky 1996, Duque 2003, Elangovan and Marimuthu 2001). Also, it has been shown that moonlight has an important role in dial and seasonal rhythms through light sensitive endogenous regulation and gene expression (Tarlow et al. 2003, Rahman et al. 2004, Takemura et al. 2006, Sugama et al. 2008).

In seabirds, the lunar cycle seems to have an important role in foraging success, chick provisioning and attendance to the colonies (Pinet et al. 2011). During mating, incubation and chick rearing, adults of some species of the Procellariidae family decrease their colony and nest attendance on brighter nights during full moon periods (Hoyo et al. 1992).

It has been widely accepted that in many cases the influence of moonlight on these birds is related to predation, since colonies of Procellariiformes are often shared with predators like skuas, gulls, raptors and crows, which have higher predation success during moonlit nights (Nelson 1989, Oro et al. 2005). By avoiding attending their colonies on nights when moonlight is more intense, they reduce their conspicuousness and increase their survival probability (Jones et al. 1989, Shealer and Kress 1991, Hoyo et al. 1992, Mougeot and Bretagnolle 2000). In some cases, moon phase does not seem to affect colony and nest attendance, but only the timing of arrival at their colony – for example, Thin-billed Prions (*Pachyptila belcheri*) from the Falkland Islands arrive later in the night during full moon (Silva et al. 2011), and Manx Shearwaters (*Puffinus puffinus*) arrive at the colony, located at the Skomer Island, southwest Wales, only after moonset on full moon nights (Riou and Hamer 2008)- which also supports that these birds adapt their return to the colony to the probability of being predated.

While in some cases both breeders and non-breeders are influenced by the lunar cycle – such as in Black-vented Shearwaters (*Puffinus opisthomelas*), for example (Keitt et al. 2004), in other occasions breeders and non-breeders may be differently influenced by this cycle (Mougeot and Bretagnolle 2000). In Thin-billed Prions and in Blue Petrels (*Halobaena caeruela*), for example, only non-breeders seem to reduce their colony attendance in moonlit nights, a behaviour that has been suggested to be due to a higher conspicuousness of non-breeders (Mougeot and Bretagnolle 2000). Whether this difference of the influence of the lunar cycle on breeders and non-breeders is variable among colonies of the same species subjected to different conditions, or if it is an inherited behaviour, is unknown.

The Bulwer's Petrels breed on several remote islands located in northern Atlantic and Pacific Oceans. On Selvagem Grande Island, this species co-inhabits with the Atlantic Yellow-legged Gull (*Larus michahellis*) (Campos and Granadeiro 1999), which is known to prey upon several seabirds, including the Bulwer's petrels (Matias and Catry 2010). Thus it would be possible that the Bulwer's Petrel adults avoid attending the colony during brighter nights when they are more easily seen by these avian predators.

The lunar cycle can also affect seabirds through its effect on prey availability, and hence have an indirect effect on the foraging success of these predators (Cruz et al. 2013). Seabirds are highly influenced by their prey distribution and some Procellariiformes species are known to change foraging strategy during their breeding period, when prey availability demands it (Magalhães et al. 2008, Paiva et al. 2010).

Previous studies about the Bulwer's Petrel diet in the Atlantic have revealed that they feed on mesopelagic species consisting of cephalopods, small squids and bioluminescent mesopelagic fish, mostly from the Myctophidae and Sternoptychidae families (Zonfrillo 1985, Neves et al. 2011, Carvalho 2012), which in turn feed mainly on zooplankton (Tyler and Pearcy 1975, Hopkins and Baird 1985, Watanabe et al. 2002). Myctophidae, Sternoptychidae and many mesopelagic species perform dial vertical migrations (DVM) between the mesopelagic (200-2000 m) and epipelagic (0-100 m) zones, migrating upwards during the night (Kinzer and Schulz 1988, Catul et al. 2011). Studies of their vertical migration patterns and that of their zooplankton prey suggest that it is strongly influenced by moonlight – they remain deeper during full moon nights (Linkowski 1996, Hernández-Leon et al. 2001, Hernández-Leon et al. 2002), and their sinking timing also seems to have a strong correlation with moonrise time (Tarling et al. 1999). Since the

Bulwer's Petrel are relatively shallow divers (rarely diving below 3 m; Mougin and Mougin 2000), they probably feed when their prey reach the near surface layers of the water during the night. So, it can be expected that on periods of full moon, when prey availability is lower, their hunting efficiency would be also lower, which would in turn affect also the chick provisioning.

Finally, the moon may also affect the at-sea behaviour of several seabird species, in different stages of their annual cycle (Roby 1991, Phalan et al. 2007, Yamamoto et al. 2008, Mackley et al. 2010, Dias et al. 2012, Cruz et al. 2013). All species studied so far revealed an increase in flight activity during nights of full moon, what may be related, as referred above, with an effect of prey availability and/or detectability (Phalan et al. 2007, Cruz et al. 2013), but also with a simple increase in flight performance (Dias et al. 2012). An on-going study on the at-sea activity of the Bulwer's Petrels has revealed similar results (non-published data).

The main aim of this study was to investigate the influence of the lunar cycle on chick provisioning of the Bulwer's Petrel from the Selvagem Grande Island colony, and thus contribute to the knowledge of the breeding ecology and behaviour of this poor studied species, and help understand the overall importance of the lunar cycle on breeding and foraging behaviour of Bulwer's Petrel and other similar species.

Methodology

Study Area

Field work was conducted on Selvagem Grande Island (30°09'N, 15°52'W), Madeira archipelago, Portugal. This oceanic island is located in the Northeast Atlantic Ocean, 163 nautical miles (≈300 km) southeast from the island of Madeira and 82 nautical miles (≈150 km) north from the Canary Islands (Figure 2). Selvagem Grande, with its 245 ha area is the largest of a group of three volcanic islands named Selvagens Islands. It has an extensive plateau 100 m above sea surrounded by cliffs, and its highest point, Pico da Atalaia, reaches 163 m above sea (Serviço do Parque Natural da Madeira 2004). This sub-tropical island is dry and warm and is surrounded by low productive waters (Alonso et al. 2012), with low chlorophyll a levels and high sea surface temperature (SST) (Paiva et al. 2010).

The Selvagens islands were classified as a natural reserve in 1971, becoming the first area of Portugal classified as such (Serviço do Parque Natural da Madeira 2004). It is also identified as an Important Bird and Biodiversity Area (IBA) (Costa et al. 2003), and in 2001 this area became part of the Natura 2000 network, being classified as a Special Protected Area (SPA) and a Special Area of Conservation (SAC) (Serviço do Parque Natural da Madeira 2013).

Selvagem Grande Island hosts a rich seabird community, which includes, besides the study species, a large colony of Cory's Shearwaters (*Calonectris diomedea*), Little Shearwaters (*Puffinus assimilis*), Madeiran Storm-Petrels (*Oceanodroma castro*), White-faced Storm-Petrels (*Pelagodroma marina*) and Atlantic Yellow-legged Gulls (*Larus michahellis atlantis*) (Campos and Granadeiro 1999).

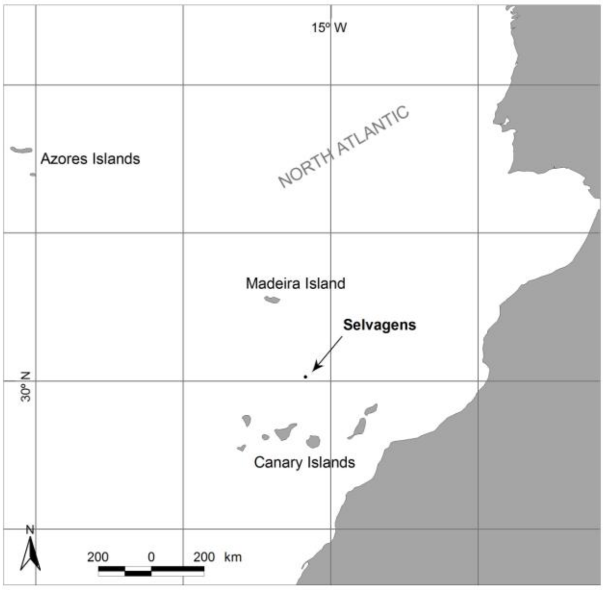

Figure 2 – Selvagens Islands location

Sampling procedures

Field work was carried out from 24th of July until 30th of September in 2009 and from the 6th of July until the 23rd of September in 2012, corresponding to the breeding season of the Bulwer´s Petrel on the Selvagem Grande Island.

A set of 77 nests was selected in 2012 at the beginning of the reproduction period of the Bulwer's Petrel (early June), and monitored until the fledging of the chicks. Nests were monitored in a week basis initially, with the frequency of the visits gradually increasing until the first hatching occurred. Since this moment the chicks started to be daily monitored, always at the same time in the morning, and in the same order. Until they fledged or died, all the chicks were weighted daily to the nearest 1 g with a spring balance, starting after the first day they were found alone in the nest after the initial brooding period (i.e., when the chick were found alone for the first time). The wing length of each chick was also measured every three days with a ruler. Nests with abandoned eggs and dead chicks were not further monitored. When chicks were absent from the nest before reaching fledging age, it was assumed that they were predated.

The data collected during a previous study, carried out in the breeding season of 2009 at the same colony, were also analysed. In this year, a sample of 61 nests was selected to be monitored. However, due to logistic reasons, data collection had only started on the 24th of July, and as such it was not possible to determine the exact hatching date for part of the chicks, or to weight all chicks since their hatching (which would have probably started in mid-July).

Statistical analysis

The hatching date of chicks in 2009 was estimated using the relationship between age and wing length, based on the data collected in 2012. A polynomial equation was fitted using the mean wing length of chicks with known age ($y=-0.0231x^2 + 2.0702x - 26.681$, $R^2=0.99$). In order to account for the potential error in age estimation (due, for example, to potential differences in growth rates between years), two additional equations were used to estimate the hatch date, based on the mean more and less SD of wing length values per age.

The influence of moon cycle on chick provisioning (measured as daily weight variation) was analyzed through chi-squared likelihood ratio tests using generalized linear mixed models (GLMMs) with normal error distributions, intercept as link function and model parameters fit by restricted maximum likelihood (REML). The fraction of the moon illuminated at midnight (hereafter "visible moon"), obtained for each sampling day from the United States Naval Meteorology and Oceanography Command (http://aa.usno.navy.mil/data/docs/MoonFraction.php), was included in all models as an explanatory variable. The daily variation in the weight of chicks (gain/loss) is known to be related to their age (Weathers et al. 2000), so age was included as a random factor in all models. To assess the relative contributions of potentially confounding variables, several models were elaborated and compared through likelihood tests until the best fitted model to the data was found. The tested models included nests as a random effect to account for individual variation, $(\text{visible moon})^2$ to allow for quadratic effects, and age class as a three-level factor as a random effect instead of chicks actual ages. For all data sets, the best fitted model had the proportion of visible moon as a covariate and age as a random effect, and the effects of other possible confoundable variables were negligible.

Typically, seabird chicks grow exponentially in the first stage of development (the “exponential phase”), after which the growth rate stabilizes (“stable phase”), to slightly decrease (in weight) just before fledging (Annex I). This pre-fledging recession (Edson 1930, Sealy 1973) - a decrease in weight before fledging - in Procellariiformes is associated with the loss of substantial accumulated fat (Reid et al. 2000) and starvation due to a decrease in parental feeding rates (Harris 1966, Ricklefs 1968, Huin et al. 2000). This is also known to happen with chicks of the Bulwer’s Petrel (Nunes and Vicente 1998; Figure 2), so since during this period parents decrease their nest attendance and chick provisioning independently from the lunar cycle, the pre-fledging period was excluded from all models in this study.

The “exponential phase” lasts for ca. 30 days in Bulwer’s petrels, (Nunes and Vicente 1998). To account for a possible differential effect of the lunar cycle on chick provisioning in different phases of the chicks growth, different GLMMs were elaborated, one for each phase (the “exponential phase” and the “stable phase”), and a third one with data for both phases. The models for the “stable phase” (both in 2009 and 2012) included only data from the 31st to 60th day after hatching, in order to include one complete lunar cycle (as done for the “exponential phase” model) and also to discard the last days of chicks permanence on the nest (the pre-fledging period, when parent provisioning has already ended). In order to consider a potential bias caused by the chick age estimation in 2009 results, all the previous analyzes were repeated using the chicks age estimated through the maximum and minimum standard-deviation of the relationship wing length - age (see details above). As the results of these additional models remain virtually unchanged, only the 2009 models using the ages estimated with the above mentioned equation are presented.

The influence of the moon phase on the chick growth was also analyzed by comparing the periods of new and full moon (defined as days with less than 30% and more than 70% of illuminated disk, respectively) during the “stable phase” of the chicks. The chick weight variation in these two periods (new and full moon) was compared using repeated measures ANOVAs. To account for the effect of chick age (see above), also two groups were considered, one including chicks hatched before the ninth day after the first hatching (coinciding roughly with the median hatching day, and also with the full moon day in both years - class I chicks), and other group including the chicks hatched after the eight day (class II chicks).

For all statistical tests, a 0.05 level of significance was considered. All statistical analyses were performed using the statistical program R (R Development Core Team 2012).

Results

Breeding success, egg and chick survival

In 2012, from the 88 initially marked nests with eggs, 39 juveniles fledged, resulting on an overall breeding success of 0.45 (*N*=88). Twenty eight eggs (31.82%) were lost, from which 15 (53.57%) were found at the nest unattended, and 13 (46.43%) disappeared from the nest. From the hatched eggs, 21 chicks died, corresponding to 35% mortality of hatched eggs: 21.67% were predated, 13.33% were found dead at the nest, most probably due to starvation.

In 2009, from the 61 followed nests, 32 juveniles fledged. 5 nests (8.2%) ceased to be followed as they became inaccessible (because chicks would hide in deep nests). So, since it is unknown if these 5 chicks fledged, breeding success was measured considering a total of 56 nests, and was 0.57 (*N*=56). Eighteen eggs (29.5%) were lost. From the hatched eggs (excluding the 5 chicks mentioned above) 6 chicks died, corresponding to 9.9% mortality of hatched eggs: 6.6% were predated and 3.3% were found dead on the nest.

Influence of moon cycle on chick provisioning

A significant relationship between the moon cycle and chick growth was found in both studied years, but only during the “stable phase” of the chick development (Table 1). In both cases, the portion of visible moon negatively affected the growth rate (Figure 3), i.e., the average daily variation in the weight of the chicks was significantly higher in periods with less moonlight. Figure 4 and Figure 5 show the growth of one chick from 2009 and another from 2012 respectively, since hatching until fledging, evidencing a decrease of the chicks weight during the second full moon period.

Comparison between new and full moon periods

The weight variation was significantly higher during new moon periods than during full moon periods (Table 2). This effect was detected in both years and in both classes of chicks considered.

Table 1- Results of the Chi-squared Maximum likelihood test for assessing the importance of moon phase on daily weight difference of the Bulwer's Petrels chicks of both 2009 and 2012.

Age class	2009				2012			
	Df	χ^2	χ^2 Df	p-value	Df	χ^2	χ^2 Df	p-value
Between 30 and 60 days	4	6.57	1	<0.05*	4	13.91	1	<0.001*
All ages	4	0.86	1	0.35	4	0.50	1	0.48
Below 31 days	4	0.26	1	0.61	4	1.28	1	0.26

Table 2- Mean (± SE) weight variation of chicks during new moon and full moon periods. *=p<0.05; **=p<0.01; ***=p<0.001

Year	Chicks group	New moon	Full moon	ANOVA
2009	Class I	1.07±2.28	-1.26±2.50	$F_{1,15}=6.44$**
	Class II	2.12± 1.58	-0.53 ± 0.86	$F_{1,14}=40.97$***
2012	Class I	2.07±2.3	-1.05±1.92	$F_{1,26}=26.18$***
	Class II	3.27 ± 2.95	-0.54 ± 3.06	$F_{1,14}=9.49$**

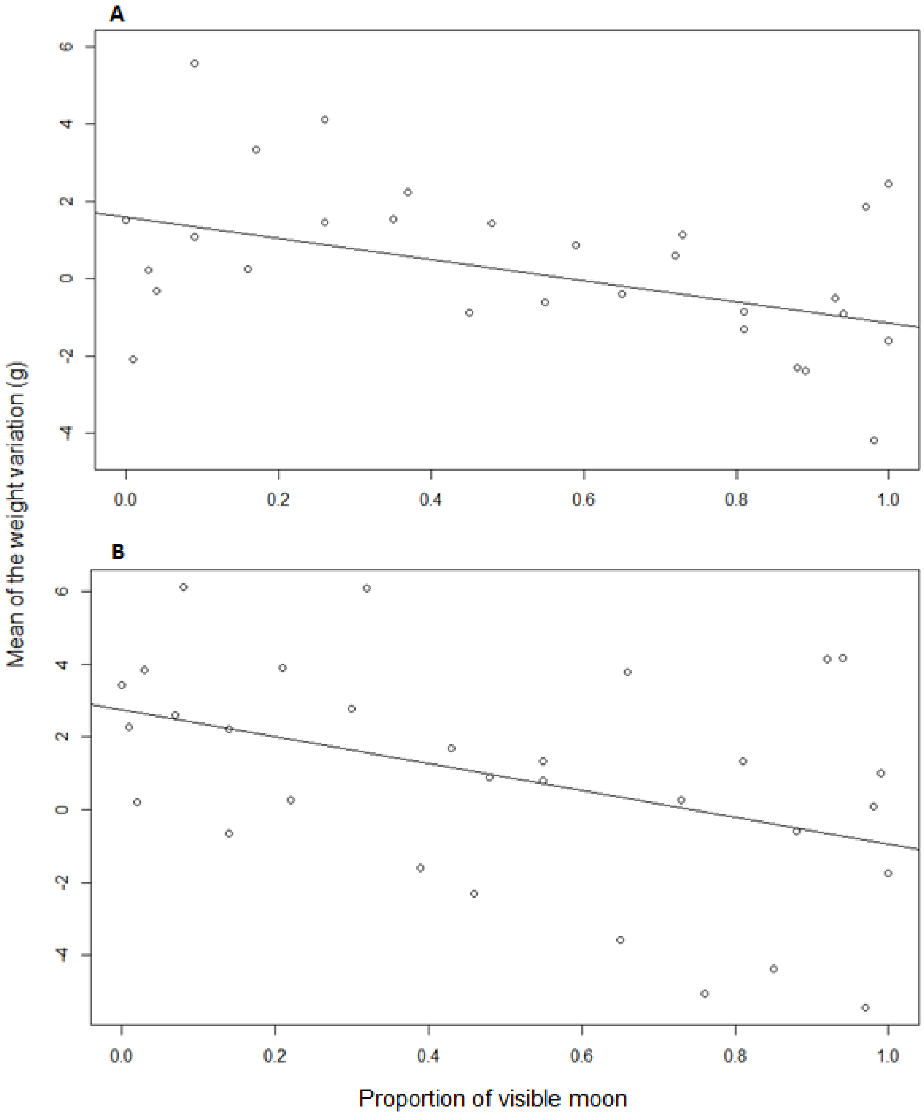

Figure 3 - Mean of the weight variation of the chicks of the Bulwer's Petrel in relation to the proportion of visible moon in 2009 (A) and 2012 (B)

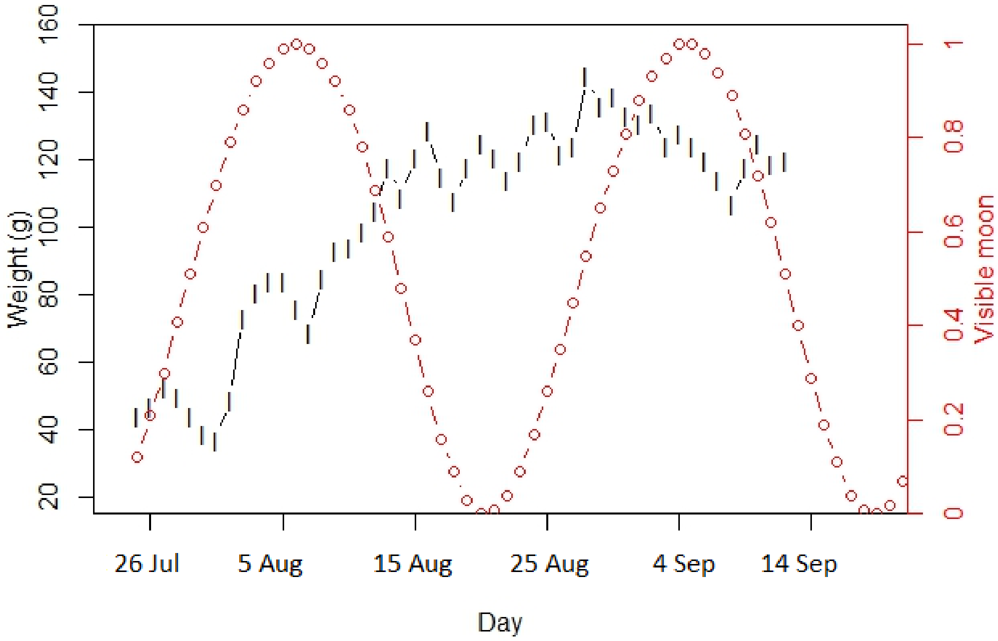

Figure 4- Evolution of a single chicks weight throughout the sampling period of 2009 and the portion of visible moon, showing a decreasing tendency on the second full moon period.

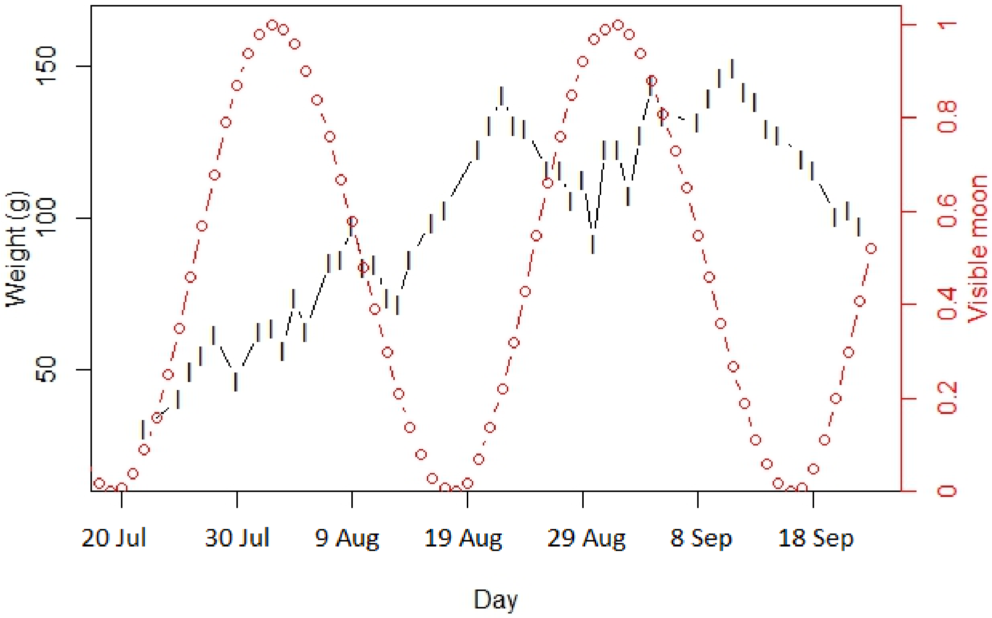

Figure 5- Evolution of a single chicks weight throughout the sampling period of 2012 and the portion of visible moon, showing a decreasing tendency on the second full moon period.

Discussion

As expected, both in 2009 and 2012, chick provisioning of the Bulwer's Petrel was influenced by the lunar cycle. However, this influence was only found during their stable growth phase, around 30 days after hatching and before they start fledging. The results have shown that during this period, not only there was a significant difference in the weight variation between full and new moon periods for all chicks, but also that the chicks weight gain decreases in nights with a higher proportion of visible moon (Tables 2 and 3). No difference was found between chicks born in different stages of the lunar cycle (i.e., before and after the new moon), regarding the influence of moon cycle on weight variation between new and full moon periods (Table 2).

Gulls, common predators on Procellariiformes colonies, are known to have a higher predation success on moonlit nights (Nelson 1989). Exclusive nocturnal activity at the colony and a decrease in nest attendance when moonlight is more intense seems to be a widely spread adaptation of many small-sized seabirds for predation avoidance by gulls (Watanuki 1986). Since the Atlantic Yellow-legged Gull existing on Selvagem Grande Island is known to predate upon Bulwer's Petrel adults, it wouldn't be unexpected that the later adopted strategies to increase their survival probability, as avoiding returning to the colony on brighter nights, which would explain a decrease in chick provisioning on nights when moonlight was more intense.

Nevertheless, it is important to highlight that the variation in the weight of the chicks, which was used as a proxy of chick provisioning, may not directly reflect nest attendance - i.e., a decrease in chicks weight does not necessarily means that a parent did not attend the nest (they could simply have brought less food, that would be not sufficient to cover the standard daily weight loss of the chicks due to their metabolism; Ramos et al. 2003). Therefore, and even though predation avoidance seems to be a plausible explanation for the observed pattern (and in accordance with what was already found in other similar species; Watanuki 1986, Nelson 1989, Mougeot and Bretagnolle 2000), research on nest attendance during the full period of chick rearing is needed to fully understand to what extent is nest attendance of Bulwer's Petrels affected by the presence of predators.

It is unknown whether avoiding nest attendance on brighter nights is an inherited specific trait, independent of predation pressure and/or other environmental factors, or if it is dependent on the conditions in each colony. The magnitude of the predatory pressure of the Atlantic Yellow-legged Gulls on the Bulwer's Petrels at Selvagem Grande is currently unknown, as it is the knowledge of the predatory pressure and the lunar cycle effect in other colonies of this species. Nevertheless, the gulls on Selvagem Grande Island are not as abundant as other predators on colonies of petrels where decreasing nest attendance on full moon night is likely to be directly related to predation avoidance. For instance, Black-vented Shearwaters (*Puffinus opisthomelas*) breeding at Natividad Island, Mexico, highly decrease their activity on brighter nights as a strategy to avoid being predated by the Western Gull (*Larus occidentalis*), whose abundance is estimated to be between 2000 and 3000 (Keitt et al. 2004). Also, on a colony of Leach's Storm-Petrels where a similar relationship between moonlight and predation avoidance was found, the number of Slaty-backed Gulls (*Larus schistisagus*) was about 3500 pairs (Watanuki 1986). The greater abundance of these predators against the estimated 12 breeding pairs and 25 non-breeders of gulls in 2010 in the Selvagem Grande Island (Matias and Catry 2010) could be an indicator that predation pressure by gulls upon the Bulwer's Petrel on the Selvagem Grande Island is low, and hence that the influence of the lunar cycle on chick provisioning is due to other factors. Further research on the influence of these gulls and other predators on the Bulwer's Petrel in different colonies, under known levels of predatory pressure, would help revealing the role of predation on the observed patterns.

Another factor that might be linked to the influence of the lunar cycle on chick provisioning is prey availability. Day-to-day variation of environmental factors is known to influence prey availability and, consequently, parents foraging success and chick provisioning through diet composition, feeding frequency and amount of food per feeding event (Peck et al. 2004, Erwin and Congdon 2007, Devney et al. 2010). Bulwer's Petrel diet consists mainly of zooplankton species that perform dial vertical migrations (Zonfrillo 1985, Neves et al. 2011, Carvalho 2012), whose magnitude is known to be negatively influenced by moonlight (Kinzer and Schulz 1988, Catul et al. 2011). Thus, the lunar cycle may also influence chicks provisioning *via* prey availability: during full moon nights prey is probably less available, what decreases parents foraging success and consequently chick provisioning, either in feeding frequency or in the size of the meals. Recent data on at-sea activity of Bulwer's Petrel from Selvagem Grande (obtained with tracking devices - geolocators) have shown that they decrease the landing rate (a surrogate for foraging activity) during the moonlit phases of the night (non-published data), which supports this hypothesis.

The reason why the influence of the lunar cycle on chick weight variation is not apparent during the first 30 days is not entirely clear. Nevertheless, other studies also revealed that moon phase do not affect nest attendance just after hatching (Bretagnolle 1990). Factors related to the chicks growth cycle might be the reason for the absence of influence of the lunar cycle on chick provisioning during this period. During the first days of age, chicks of Procellariiformes grow at a higher rate, consuming larger amounts of food, and also gradually increase their ingestion capacity until reaching their stable growth phase. Because of this, parents also gradually increase feeding frequency (Barrett et al. 1987, Hamer et al. 1997, Quillfeldt and Peter 2000) and meal size (Bolton 1995), which may mask a possible influence of the lunar cycle.

It is clear then that the lunar cycle influences chick provisioning of the Bulwer’s Petrel. However, further studies, focusing this topic in this and in other colonies, are necessary to fully understand the patterns observed. Whether they are due to a behavioral adaptation characteristic of the Bulwer’s Petrel species or uniquely from this colony, or/and if it is simply a result of exogenous environmental factors such as prey availability is yet to be understood.

III. The brood guarding behaviour in Bulwer's Petrel

Introduction

During the days after hatching, seabird chicks are frequently attended by at least one of the parents, a behaviour that is generally referred to as brood guarding. The duration of the brood guarding period is highly variable between species (Ricklefs and Roby 1983, Varpe et al. 2004), ranging from less than a week in some small petrels (Imber 1976, Boersma et al. 1980) to almost 40 days in some albatrosses (Catry et al. 2006, 2010).

Brood guarding allows the newly hatched heterothermic chick to maintain its body temperature until it reaches homeothermy (Bech et al. 1991, Visser 1998, Weathers et al. 2000), greatly reducing chicks thermoregulatory energy costs (Klaassen 1994). However, parents have to face a trade-off between brood-guarding and foraging - with only one parent being able to forage, energy acquisition is hardly maximized, leading to a reduction in food acquisition for both the parents and the chick (Weimerskirch and Lys 2000, Catry et al. 2010).

In many species chicks can be brood-guarded for longer than the time needed to reach homeothermy (Warham 1990, Catry et al. 2009), which suggests that brood-guarding is important in other ecological functions related to the chick survival and condition. In fact, a positive relationship between brood-guarding duration and chicks fledging probability has been observed (Tveraa and Christensen 2002, Catry et al. 2010). Some hypotheses have been suggested to explain this link. Many studies support the *synchronisation hypothesis*, which states that burrow-nesting seabirds benefit from synchronized hatching when predators are present, due to a less probability of being predated by a dilution effect (Catry et al. 2009). Following this hypothesis, a seasonal decline in brood guarding duration should therefore exist, but only in populations subjected to a predation pressure in the colony. This effect is clear for example in the Black-browed Albatrosses (*Thalassarche melanophrys*) that co-inhabit with Southern Skuas (*Stercorarius antarcticus*), in which a pronounced seasonal decline in brood-guarding duration was found (Catry et al. 2010). Also, in Grey-headed Albatross (*Thalassarche chrysostoma*) early and late chicks suffered higher mortality (Catry et al. 2006), suggesting the inexistence of predator swamping by chicks born far from the peak of hatchings. Additionally, early hatching chicks of the Antarctic Petrel (*Thalassoica antarctica*) have lower survival probability than late hatching chicks, which was suggested to be related to higher predation risk in the first case (Varpe and Tveraa 2005). These results suggest that these populations benefit in breeding synchrony and that it is linked to predation risk, providing strong support to *synchronisation hypothesis*.

Another possible explanation for an extended brood-guarding duration is the existence of an energy-saving and regular provisioning strategy, associated with the increase of the metabolic rate when homeothermy is achieved - the *growth assistance hypothesis* (Catry et al. 2009). This hypothesis predicts that chicks brood-guarded for longer periods will grow faster and attain larger body sizes than chicks with the same age but brood-guarded for less time. It assumes that a continuous nest attendance might result on the provision of more regular smaller meals to the recently hatched chick (that has small guts and fast digestion rates) and, as an energy-saving strategy, will help an efficient use of the energy by the chick, allowing it to increase body mass at a higher rate. An example is the Snow Petrel (*Pagodroma nivea*), in which the brood-guarded chicks have a higher body mass at day 4 comparing to those unattended by their parents (Amundsen 1995).

Life history theory states that parental care is a trade-off between current and future reproduction (Roff 1992). In many cases, parents also seem to adjust brood-guarding duration and behaviour to their own body condition; as consequence, parents with lower body conditions tend to stop brood-guarding earlier (Tveraa et al. 1998, Tveraa and Christensen 2002), as do also those with more probability of breeding in the future (Heidinger et al. 2006). In some cases, parents also seem to be able to adjust the brood guarding period to the body condition of their chicks, but only if that would not compromise their own fitness (Catry et al. 2006).

Predation and body condition (of both parents and chicks) seem to be the main factors affecting the decision of parents to stop brooding. However, other factors as prey availability (Roby 1991) and harsh weather conditions (Weathers et al. 2000, Hodum 2002) also might have an impact on brood-guarding duration. How species cope with these several factors probably depend on their own body size, which determines their ability to nest in sheltered places. Larger species usually nest in more exposed areas, and so brood-guard for longer periods (Weathers et al. 2000). The factors mentioned above are not necessarily mutually exclusive, and whether they act together or separately in the regulation of brood guarding behaviour depend not only on environmental factors but probably also varies among colonies and life history characteristics (Chastel et al. 1995, Weathers et al. 2000).

The main aim of this study was to analyse the brood-guarding behaviour of the Bulwer's Petrels breeding in Selvagem Grande Island. Specifically, the relationship between brood-guarding duration and hatching date, chick condition, survival probability and moon cycle were studied. Although widespread among several seabird taxa, the mechanisms underlying brood-guarding duration and factors affecting parents decision to stop brooding remain yet mostly unknown, and so the results of this study will contribute to understand which factors might be influencing the trade-off between brood guarding and parental survival, and whether predation or other factors are affecting brooding duration.

Methodology

Sampling procedures

The sample set analysed in this study was the one collected in 2012, described in the previous chapter, after excluding the chicks that were predated on hatching day by Madeira lizards *Teira dugesii*. The field work was conducted during the breeding season of the Bulwer's Petrel on the Selvagem Grande Island, from the 6th of July until the 23rd of September in 2012.

All the nests (n=58) were checked every day, and continuous nest attendance by the parents on the first days after hatching was registered. Chick mass at the fifth day after hatching was measured with a spring balance (to the nearest 1 g).

Statistical analysis

Brood guarding duration was defined as the number of subsequent days that chicks were found attended by their parents after hatching. Since no chick was brood guarded for more than 4 days, the variable Mass5, defined as the mass of the chicks at day 5 after hatching, was used as a proxy of their body condition. All data were previously tested for homoscedasticity and normality, and further analyses were conducted accordingly. An analysis of variance was performed to compare Mass5 of chicks brood guarded for less than two days (0 or 1 day), for two days and for more than 2 days (3 or 4 days). A Wilcoxon rank sum correlation test was used to analyse if brood guarding days influenced the final survival of the chicks. A Spearman's rank correlation was used (using the hatching date of the chicks) to check for a seasonal variation in brood guarding duration. A Pearson's correlation was performed to test the relationship between hatching day and mass5 and a t test to compare hatching dates of chicks that fledged or not.

Hatching period ranged 16 days (from 10th to 26th of July), with the first chicks hatching during waning gibbous (around 0.6 of visible moon), and the last on waxing quarter (around 0.5 visible moon), having peaked right before new moon. In order to account for a possible effect of the moon phase on Mass5, a t-test was performed comparing mass5 of chicks born during and outside the new moon period (less than 30% of moon visible at midnight).

All statistical analysis was performed on statistical software R (R Development Core Team 2012). For all statistical tests, a 0.05 level of significance was considered.

Results

Brood guarding duration varied from 0 to 4 days (1.56 ± 0.89, *n*=57). It had no influence on Mass5 (F=1.62, df=49, p=0.21) (Figure 6) nor on chicks survival (W=375.5, p=0.53). Chicks survival was also not influenced by hatching date (t=0.039, df=21.35, p=0.96). However, there was a seasonal trend between hatching date of the chicks and brood guarding duration (S=27207.14, *r*=-0.31, p <0.05) (Figure 7), and also a correlation between hatching date and Mass5 (t=3.07, df=48, *r*=0.41, p<0.01) (Figure 8). Mass5 of chicks hatched during new moon period were significantly higher than those hatched outside this period (t=-2.22, df=47.99, p<0.05) (Figure 9).

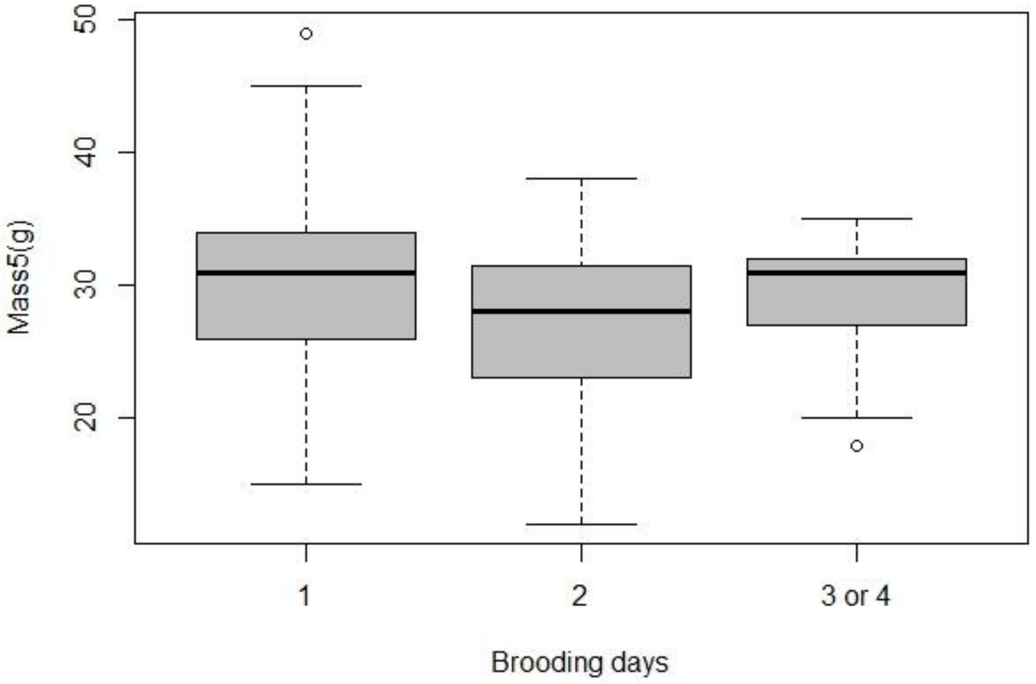

Figure 6 - Relationship between brood guarding duration and weight of the Bulwer's Petrel chicks on the fifth day after hatching (Mass 5).

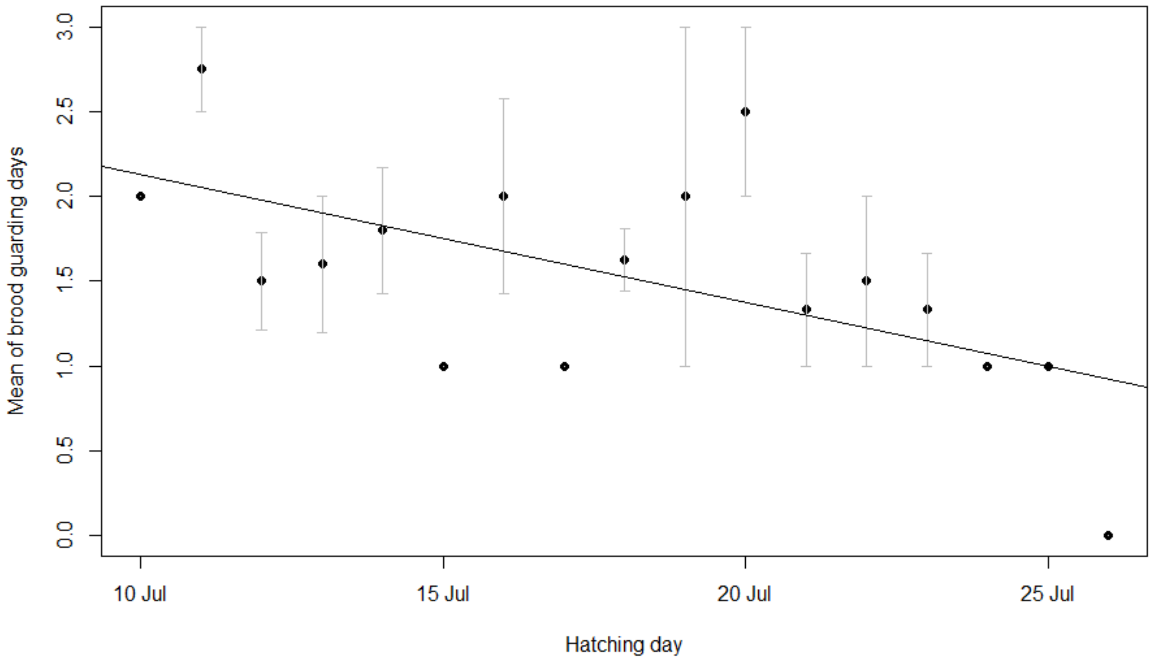

Figure 7 - Relationship between brood guarding duration (in days) and hatching day of the Bulwer's Petrel chicks in 2012 (S=27207.14, *r*=-0.31, p <0.05).

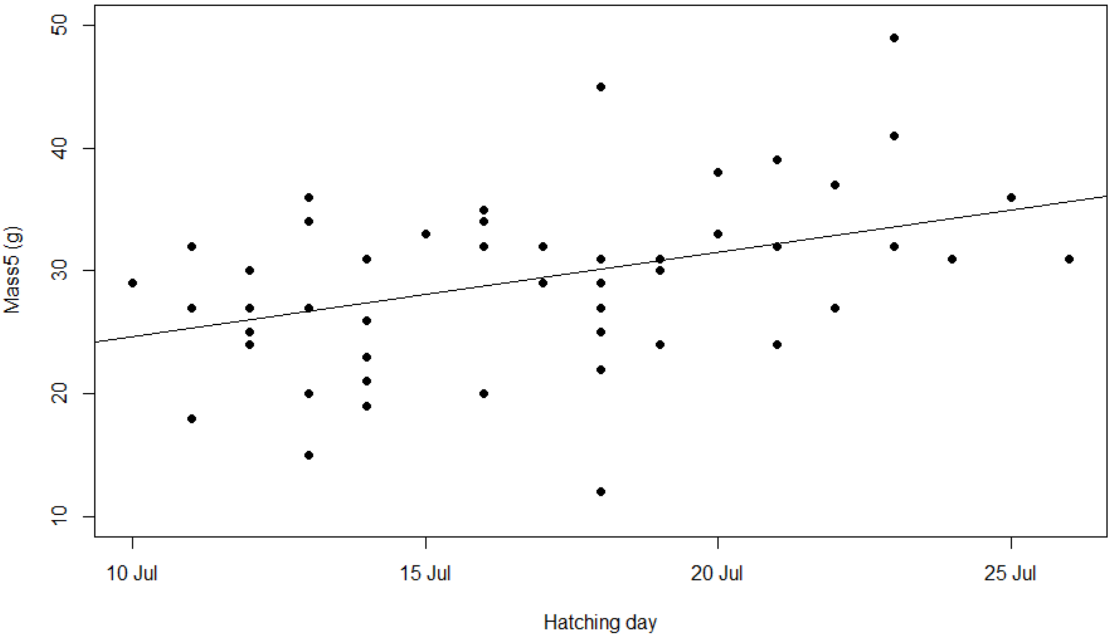

Figure 8 - Relationship between the weight of the chicks 5 days after hatching (Mass5) and hatching day of the Bulwer's Petrel chicks in 2012 (*r*=0.41, p<0.01).

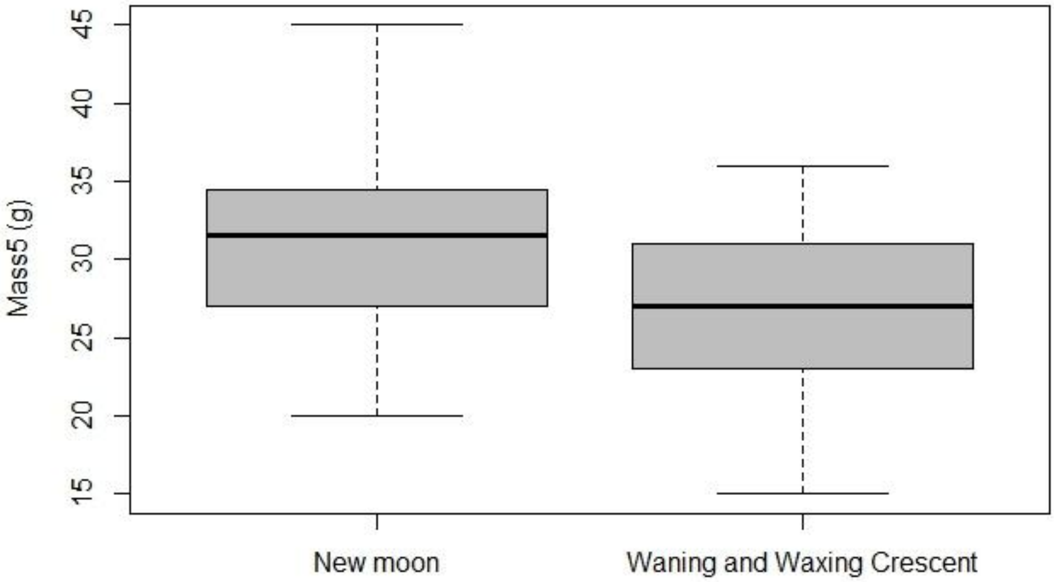

Figure 9 - Boxplot of the mass of the chicks on their fifth day after hatching (Mass5) in relation to the moon phase of the day they hatched - new moon period (less than 0.3 of visible moon), and before and after the new moon period (Waning Crescent and Waxing Crescent respectively).

Discussion

A significant decreasing seasonal trend was found on the duration of the brood guard, i.e. chicks hatched later were brood-guarded for less time than those hatched earlier in the season. The fact that Mass5 has not been influenced by brood-guarding duration (Figure 6) suggests that brood-guarding does not play any role in achieving higher mass growth rates on the first days of life of the chicks, as stated by the *growth assistance hypothesis* (Catry et al. 2009; see Introduction). To our knowledge, the only evidence supporting this hypothesis comes from a study conducted in the Antarctica, with Snow Petrels (Amundsen 1995). Chicks growing in these extremely cold environments experience much higher energy expenditures to maintain body temperature and basic metabolic functions (Hodum and Weathers 2003), comparing to those chicks of species living in warmer temperatures, such as those existing in temperate Atlantic, where Selvagem Grande Island is located. Thus, it is probable that the energy saved by the chicks of the Bulwer's Petrel through longer brood guarding duration would not counterbalance the reduction of chick provision due to brood guarding

The decreasing seasonal trend in brood guarding duration found in this study supports the *synchronization hypothesis* (see Introduction). Chicks of the Bulwer's Petrel are known to be predated not only by Atlantic Yellow-legged Gulls (Matias and Catry 2010) but also by the Madeiran Wall lizards (*Teira dugesii*), highly abundant in Selvagem Grande Island (Matias et al. 2009). At least three chicks from our study sample were predated by lizards, of which two were unattended at the time, suggesting that brood guarding might be important in protecting the newly hatched chicks from such attacks.

Even though it is known that older chicks can be predated by both gulls and lizards (Matias et al. 2009, Matias and Catry 2010), in the present study predation was mostly found upon very young chicks, suggesting that they are particularly vulnerable during their first few days after hatching. To maximize the survival probability of their chicks, parents with early hatching chicks probably remain more time at the nest until more chicks hatch, as a swamping predator strategy.

A similar study, performed with Cory's Shearwaters also in the Selvagem Grande Island, showed no seasonal trend in brood-guarding duration (Catry et al. 2009). However, to our knowledge there is no record of chicks of Cory's Shearwaters being predated by the

Atlantic Yellow-legged Gulls, and even though predation by lizards has been found, it occurs especially while chicks are hatching or right after hatching (Matias et al. 2009), a time when parents would probably still brood-guarding, independently of predation. The contrasting patterns between these two species in the same colony might suggest that, when predatory pressure is present, parents adopt predator swamping strategies (in this case, increasing brood-guarding duration in early hatched chicks), as a way to increase the survival probabilities of their chicks. This gives further support to the *synchronization hypothesis*.

No relationship was found between brood-guarding duration and chick survival. This suggests that Bulwer's Petrels may be able to adapt brood-guarding duration to the exact time needed for maximizing the chances of chick survival or, alternatively, that it is simply an inherited trait, with no longer influence on chicks survival. However it can also mean that the variation in duration of this behaviour is due to other factors other than the goal of "swamping" predators.

Mass5 was found to be dependent on the hatching day. This variable was not dependent on brood-guarding duration, but was related also with moon phase (Fig.8): chicks hatched during new moon had higher masses than those hatched outside this period. This suggests that the difference between Mass5 of chicks hatched in different days might be due to the lunar cycle, due to the same reasons investigated and discussed in chapter II. Nevertheless, no relationship was found between chick provisioning during the first 30 days after hatching and the lunar cycle (see chapter II). The apparent contradictory result obtained here may be explained by the fact that on the first five days after hatching there is a high probability of receiving a very reduced amount of food (in some cases receiving just one meal from only one of the parents, since the other parent had spent most of this time brood-guarding). Consequently, any little influence in parents foraging success is more easily perceived in chick provisioning during this period than in the subsequent days of the chicks life. It is important to note, however, that factors other than the lunar cycle (e.g. short-term variations in oceanographic or weather conditions) might be affecting the results, considering that only 16 days were analysed.

IV. Conclusion

Marine birds, as the Bulwer's Petrel, are highly influenced by external factors such as prey availability, predation and weather (Diamond and Devlin 2003, Piatt et al 2007). These factors commonly undergo fluctuations; however, due to the on-going major environmental changes resulting from human activities (such as pollution, tourism, fishing among others), both biological and oceanographic conditions have been subjected to an increasing variation, which in turn affects seabird populations (Thompson and Ollason 2001, Frederiksen et al. 2004, Parmesan 2006). Knowledge on how species will react to this variability is needed not only for understanding the future of marine bird populations, but also to help in possible future conservation decisions.

Even though the breeding distribution and chronology of Bulwer's Petrel is already relatively well known, the influence of environmental factors and their variability, and the impact of crescent human activity on this species, are far from being unravelled. In this study it became clear that the lunar cycle influences chicks provisioning and that brood guarding seems to have an important ecological function. The knowledge related with the importance of environmental factors, such as the lunar cycle, and of behaviours such as brood guarding, on the species breeding biology, will allow for a better understanding of the Bulwer's Petrel population dynamics and ecology. Such information is also of major importance in forecasting how this species will be able to react to changes in environmental conditions, such as those induced by human activities, and how this might affect populations survival and distribution. For instance, learning that adults respond to changes in factors affecting prey availability (possibly such as the lunar cycle, as discussed in this study), will contribute not only to understand the behavioural and biological adaptations of the Bulwer´s petrels facing various prey availabilities and distributions, but also how the variation in factors determining prey availability may affect the survival and dynamics of this and other similar species.

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Annex I

Growth of two study chicks: from 2009 (A) and 2012 (B)