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WHEN THE FLEDGLINGS RED-FOOTED BOOBIES (*Sula sula*) ACQUIRE FLIGHT CAPACITY

Marcelo Câmara Rodrigues [1*], *Arrilton Araújo* [1] *& Maria de Fátima Arruda* [1]

[1] *Universidade Federal do Rio Grande do Norte (UFRN), Laboratório de Ecologia Comportamental, Programa de Pós-Graduação em Psicobiologia. Caixa postal 1511, Campus Universitário, Natal, RN, Brasil. CEP: 59078-970*
E-mails: cr.marcelo@gmail.com, arrilton@gmail.com, mariadefarruda@gmail.com

ABSTRACT

The high cost of parental care may sometimes result in a conflict of interest between parents and offspring. To achieve the benefits of producing viable offspring and/or additional breeding opportunities, tropical seabirds must be able to afford the costs of searching for food in an oligotrophic environment. In order to verify the behavioral variation of Red-footed Boobies (*Sula sula*) during the late phase of its development, over a 12 week period was recorded the behavior of 15 fledglings. The behavioral records were made with the instantaneous focal animal method in windows of 15 minutes and records every minute. Records of feeding, agonism and frigates attacks were recorded *ad libitum* during the days of observation. No differences in the frequency of activities displayed by offspring at advanced stages of fledgling development, or in the frequency of parental presence during the transitional period to full capacity for flight were detected. On the other hand, it was observed that fledglings synchronized their presence at the nest with that of the adults even after achieving full flight capacity and that during periods of absence neighboring offspring were likely to occupy vacant nests. We speculate that with this behavior they apparently are trying to acquire, opportunistically, extra food resources from other, not directly related adults. However, we did not observe any fledgling being fed by a non-related adult. We also recorded the expression of aggressive behaviors of a fledgling towards a neighboring fledgling on the nest. These observations suggest the presence of a behavioral strategy in this species that is motivated by the continuously high demand for sustenance as the frequency of parental provisioning declines during the more advanced stages of offspring development. Although we did not verify changes in the fledglingsô behavioral repertoire, the occurrence of agonistic behavior among them suggests that they must try alternative strategies to get food while not quite ready to live independently.

Keywords: behavioral activities; development; emancipation; feeding; flight.

INTRODUCTION

Parental care, despite being costly for breeding adults, represents a beneficial investment of energy when it increases individual fitness, as reflected in offspring survival and future reproductive success. A conflict of interest arises in this situation, whereby adults try to minimize their necessary investment in parental care and offspring try to reap the maximum possible benefits of receiving parental care, leading to the emergence of alternative behavioral strategies (Trivers 1972). One such strategy is nest parasitism, in which the costs of parental investment are transferred to other individuals. However, anti-parasitic strategies of hosts may end up counterbalancing the extra benefits that a parasite can derive in not caring for their own offspring (Lezalová-Piálková 2011, Calderón *et al.* 2012). In species characterized by alloparental care, there is a division in the costs of caring for offspring among individuals that breed in close proximity to one another or that have a level of kinship that justifies their investment through increased inclusive fitness. In the first situation, adults spend part of their time and effort caring for offspring with which they have no immediate kinship, in return for the benefits afforded to their own offspringôs survival acquired through the similar investment in parental care by unrelated adults (Lecomte *et al.* 2006, Beaulieu *et al.* 2009). Thus, environmental pressures directly shape the reproductive strategies and life history attributes that characterize a particular species.

Red-footed Boobies (*Sula sula*) are markedly pelagic seabirds of the family Sulidae that inhabit tropical ocean environments, building their nests in the canopy of trees or shrubs; clutch size is only one egg that is incubated by both parents, which alternate the duty (Nelson 1978, Carboneras 1992). Sulides are large-bodied, colonial breeders with altricial young that require a long period of direct parental care (90 to 190 days) that extends well into the fledging period to sometime after achieving the capacity for flight (Carboneras 1992, Stark & Ricklefs 1998, Bried & Jouventin 2001).

Tropical oceans are comparatively less productive than the subtropical ones, with a cycle of food resource availability that is often punctual and relatively random, increasing the necessary time dedicated to foraging by many seabird species and, hence, imposes a higher cost of investment in parental care (Weimerskirch *et al*. 2005). As a means of compensating for the nature of resource availability in tropical ocean environments, many birds that breed in that region have relatively low fecundity (Hamer *et al*. 2001, Jetz *et al*. 2008, Mannocci *et al.* 2012). The necessity of making long foraging trips that characterizes many pelagic species also has a direct influence on typical avian life history attributes, such as reduced brood sizes (Bried & Jouventin 2001). Tropical oceans should favor the evolution of reproductive behavioral strategies that help to attenuate the higher cost of parental care in such environments.

The objective of the current study was to investigate the occurrence of behavioral variation during the later stages of fledgling development, in particular, during the transition to achieving flight capacity in Red-footed Boobies. To this end, we recorded the behavioral repertoire in the pre- and post-flight phases of the Red-footed Boobies fledglings.

MATERIAL AND METHODS

Study area

Data were collected on the main island of the Fernando de Noronha archipelago, located 360 km off the northeastern coast of Brazil. The island is characterized by a semi-arid climate with a rainy season lasting from February to August and a dry period from September to January. Behavioral observations were conducted over a period of 12 weeks from August to October of 2005. The study area was divided into two sites located on the northwest side of the archipelago, the cliffs of Dolphin's Bay (3º51'29"S, 32°26'48"O) and the cliffs of Sancho's Bay (3º51'15"S, 32º26'32"O), facing the continent and with free access by tourists, but without any sort of urbanization or other development.

Procedures

Behavioral observations were initiated during the later stages of the species' breeding period, which typically starts in March and April (Schulz-Neto 2004). The approximate ages of individual Red-footed Booby fledglings were estimated based on the known patterns of plumage development in the species, according to Martins & Dias (2003). We observed 15 nests, in the canopy of trees close by about seven meters from the ground and an average distance of 10 m from the observer. The nests were distributed between the two sampling points, focusing on stage 3 individuals, at which time the remiges are becoming visible amongst the plumage, until they reached stage 5, when the plumage is dominated by the first molt to dark brown feathers, which characterizes juveniles in this species. For the purpose of recording behaviors, the fledgling subjects were grouped by two conditions: pre-flight, when the bird had not yet left the nest, and post-flight capacity, when the bird was observed leaving or returning to the nest by flying. The assignment of each individual to one of these two conditional groupings was determined by its first recorded absence from the nest site.

The 15 nests were divided into three groups of five and observed on a weekly basis throughout the duration of the study period. Each group of five nests was observed on a total of 15 different occasions, for a total of 45 days of observation. Behavioral observations during the day were divided into four shifts: early morning (06:00 to 09:00 h), late morning (09:00 to 12:00 h), early afternoon (12:00 to15:00 h) and late afternoon (15:00 to 18:00 h). All nests in each group were observed during each of the four daily shifts. To avoid observing each nest during the same time periods every day, the first nest observed on the first day in each group was shifted to the position of last nest observed in the sequence on the second day, and so on. This rotation was applied for the duration of the study, resulting in three observation trials for each nest, during each of the observation periods. Under this behavioral sampling scheme, a total of 900 individual observation periods, lasting 15 min each, for a total of 225 hours of observation, were recorded.

Due to the restrictions imposed by our license to carry out data collection in the study area, we were not allowed to handle the animals. So, no markings or measures were performed on them.

Behavioral categories and observation methods

Two methods were used to record the behavior of birds during the data collection. The instantaneous focal animal method (Martin & Bateson 1994) with 15 minutes observation windows and records every minute was used to compare the behavioral frequencies of offspring between the two stages of development considered here: pre-flight and post-flight. Behaviors recorded were resting, handling material, preening, exercise, and roosting. Less frequent behaviors for each individual, such as feeding, agonism, and frigate bird attacks, as well as arrivals and departures of the Red-footed Boobies fledglings in the nests were recorded every time they were observed, through *ad libitum* sampling over all day watching. Behavioral categories, such as resting, preening, exercising, and feeding were based on Nelson (1978); additional categories - handling material, roosting, frigatebird attack, and agonism - were included after pilot observations (Table 1).

As the frigatebirds are a species of birds known for stealing the boobies' food when they are returning from foraging areas (Le Corre & Jouventin 1997), frigate attack has been included as a behavioral category once it represents an interaction between a booby and a frigatebird that is directly related to obtaining food.

Table 1. Behavioral categories with definitions, and observational sampling methods used in the Red-footed Boobies (*Sula sula*) study.

Behavioral Categories	**Definitions**	**Observational Sampling Method**
Resting	When the bird was perched in a tree and not interacting with the surrounding environment, defined as resting and sleeping by Nelson (1978).	Instantaneous Focal Animal
Handling Material	The bird was in a tree, manipulating nest material, branches, leaves, or flowers in the vicinity.	Instantaneous Focal Animal
Preening	The bird was in a tree actively preening their feathers and scratching, defined as preening and associated behavior by Nelson (1978).	Instantaneous Focal Animal
Exercising	The bird was stretching, moving its wings, or making short flights from the perch, defined as moving and exercising by Nelson (1978).	Instantaneous Focal Animal
Roosting	The bird was perched, but attentive to its surroundings.	Instantaneous Focal Animal
Feeding	The bird was soliciting or receiving food from an adult (Nelson 1978).	Behavioral Sampling
Frigatebird Attack	The bird (fledgling or adult) was pursued and/or attacked by raiding frigatebirds.	Behavioral Sampling
Agonism	The bird displayed aggressive behavior towards a neighboring fledgling on the nest.	Behavioral Sampling

Statistical analysis

We compared behavioral data of two late stages of the fledgling developmental period: (1) pre-flight capacity stage and (2) post-flight capacity stage. All of the behavioral records were grouped and divided according to the number of days of observations, because one day represents a single sampling unit. In chi-square test the data was grouped and divided only among the shifts.

Feeding, agonism, and frigatebird attack were recorded along four shifts throughout the day, for any individual visible from the observation point, and compared using the chi-square (X^2) test, while the frequencies of activities (Resting, Material Handling, Preening, Exercising, and Roosting) between the two stages of fledgling development, only for the 15 Red-footed Boobies fledglings that were being watched, were grouped by day and analyzed with the Mann-Whitney (U) test. The presence of fledglings at the nest site and the frequency of arrivals and departures between shifts were compared using the Kruskal-Wallis (H) test and *a posteriori* with the Mann-Whitney test. All of the statistical analyses were performed using the SPSS 14 software package.

Despite the same individual subjects being the focus of study in both the pre-flight and post-flight stages, the duration of each stage was different for each individual, resulting in different sample sizes for each subject, characterizing the data set as consisting of unpaired samples. For all two-tailed statistical tests the probability value was set at $p \leqslant 0.05$.

Table 2. Comparison of the absolute frequencies of fledgling behaviors between the two discrete stages of later development of the Red-footed Booby fledglings. In parentheses are their respective values of relative frequencies.

Fledgling Behavior	Pre-flight Capacity	Post-flight Capacity	Mann-Whitney test
Resting	1488 (27.12%)	1505 (23.58%)	U = 327.0; p = 0.13
Material Handling	91 (1.66%)	28 (0.44%)	U = 41.5; p = 0.22
Preening	1529 (27.87%)	1649 (25.83%)	U = 388.5 ; p = 0.57
Exercising	32 (0.58%)	54 (0.84%)	U = 125.5 ; p = 0.81
Roosting	2346 (42.76%)	3143 (49.24%)	U = 315.5 ; p = 0.09

RESULTS

The frequency of records for the presence of Red-footed Booby parents together with their offspring at the nest was only 8% of the records occurring during all period of the study, with no detectable difference between the pre-and post-flight stages (U = 104.00; p = 1.00).

The fledglings showed no variation in the frequency of the behavioral categories recorded between the pre- and post-flight stages: resting (U = 327.0; p = 0.13), handling material (U = 41.5; p = 0.22), preening (U = 388.5; p = 0.57), exercising (U = 125.5; p = 0.81), and roosting (U = 315.5; p = 0.09) (Table 2).

A comparison of activities related to food acquisition between the shifts showed that feeding ($X^2 = 31.33$, $p < 0.01$), frigatebird attack ($X^2 = 11.97$, p = 0.01), and agonism ($X^2 = 10.08$, p = 0.02) were more frequently observed during the last shift (Figure 1). The fledgling only have access to other nests through the flight, so there is no occurrence of agonism between the fledglings in the pre-flight phase.

Of the 15 fledglings observed, 11 reached full flight capacity at stage 4 of development, when less than half of their bodies were covered with the characteristic juvenile plumage, while 4 birds achieved full flight capacity at stage 5, when their whole bodies were covered with the juvenile plumage.

During the post-flight capacity stage, we found that the presence of the fledglings at the nest varied between shifts (H = 8.90; p = 0.03), being recorded more frequently during the early morning and late afternoon shifts (Figure 2a). Both shifts showed higher frequencies of fledglings presence at the nest compared to the early afternoon shift, while the frequency was also higher during the early morning shift compared to late morning (Table 3). On the other hand, only a few parents were observed at the nests during the period of observation window. Usually they left before 06:00 h, returning only after sunset, about 17:30 to 18:00 h.

Table 3. Results of the Mann-Whitney test comparing the frequencies of presence, arrival, and departure of the Red-footed Boobies fledglings for the nest between the shifts of behavioral sampling. Shifts: Early morning = 06:00 to 09:00 h; Late morning = 09:00 to 12:00 h; Early afternoon = 12:00 to 15:00 h; Late afternoon = 15:00 to 18:00 h. Significant probability value at p ≤ 0.05 in bold.

	Presence		**Arrive**		**Departure**	
Sampling Shifts	**U**	**p**	**U**	**p**	**U**	**p**
Early Morning x Late Morning	405.0	**0.04**	80.0	0.87	130.0	**0.03**
Early Morning x Early Afternoon	361.0	**0.01**	49.5	**0.03**	102.5	< **0.01**
Early Morning x Late Afternoon	562.5	0.84	71.5	0.33	115.0	0.25
Late Morning x Early Afternoon	497.5	0.54	204.5	< **0.01**	328.0	0.09
Late Morning x Late Afternoon	440.0	0.12	268.5	0.26	246.0	0.45
Early Afternoon x Late Afternoon	399.5	**0.04**	292.0	0.06	207.0	**0.04**

The frequency of fledglings arriving at (H = 10.65; p = 0.01) and leaving (H = 12.41; p < 0.01) the nest site also varied between shifts (Figures 2b and 2c). The arrivals at the nest of fledglings were higher in early afternoon shift compared to early and late morning shifts (Figure 2b). With respect to offspring departures from the nest, the observed frequency of this behavioral category was higher in early afternoon shift compared to the late afternoon and early morning shifts; also, the frequency of departures from the nest was higher in late morning compared to early morning shift (Figure 2c).

DISCUSSION

As expected, Red-footed Booby fledglings in the later periods of parental care and transitioning to independence did not differ in their behavioral repertoire between the pre and post-flight stages, suggesting that it already has its full development (Dütmann *et al.* 1998). The highest frequency of adult presence with fledglings at the nest occurs soon after egg laying and decreases steadily over the advanced stages of parental care. With respect to the behavioral repertoire, offspring exhibit greater dependence on parental care during the earliest periods of development, and throughout it, new activities begin to emerge that indicate greater independence from their parents (Dütmann *et al.* 1998). We did not find any differences between the frequencies of behavioral activities displayed during the pre- and post-flight stages, which was expected in offspring during the early stages of fledgling development, with respect to protection and temperature maintenance.

From all behavioral categories analyzed here, the behavioral categories “arrival at the nest”, “departure from the nest”, and agonism were only recorded after the fledglings had developed its flight capacity. Agonism draws most attention because of its possible relation with food acquisition by the fledglings. In cases where a nest was occupied by a neighboring fledgling when the resident offspring returned, we typically observed an aggressive exchange of pecks and the intruder submitted by moving to their own nest (agonism). The low level of aggressiveness displayed by the intruder also supports the idea that their occupation of neighboring nests is opportunistic. Since the mortality rate of fledglings is greater during the development of flight and foraging capacity (Hamer *et al.*2001), it is also important to consider that the probability of a neighboring offspring having died, and the associated potential for acquiring additional provisions from neighboring adults, also increases.

The observations of the current study also show that as their flying abilities improve, fledglings begin to synchronize their presence at the nest site with that of the adults. We suggest that this strategy helps to ensure that food may still be acquired, especially while foraging forays may reach limited success in capturing and actually ingesting prey during the early stages of developing the full capacity for sustained flight.

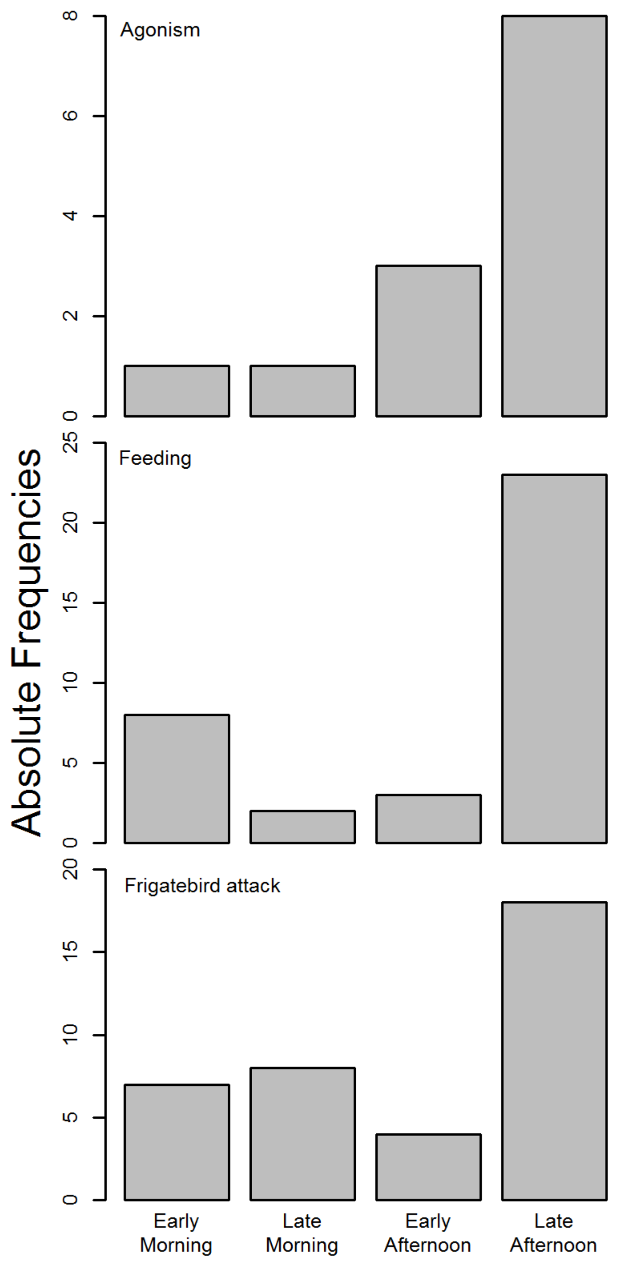

Figure 1. The absolute frequencies of food-related activities recorded in the study area across the four daily sampling shifts. Activities that showed significant differences according to the Chi-square tests included: agonism ($X^2 = 10.08$ and $p = 0.02$), feeding ($X^2 = 31.33$ and $p < 0.01$) and frigatebird attack ($X^2 = 11.97$ and $p = 0.01$). Shifts: Early morning = 06:00 to 09:00 h; Late morning = 09:00 to 12:00 h; Early afternoon = 12:00 to 15: 00 h; Late afternoon = 15:00 to 18:00 h.

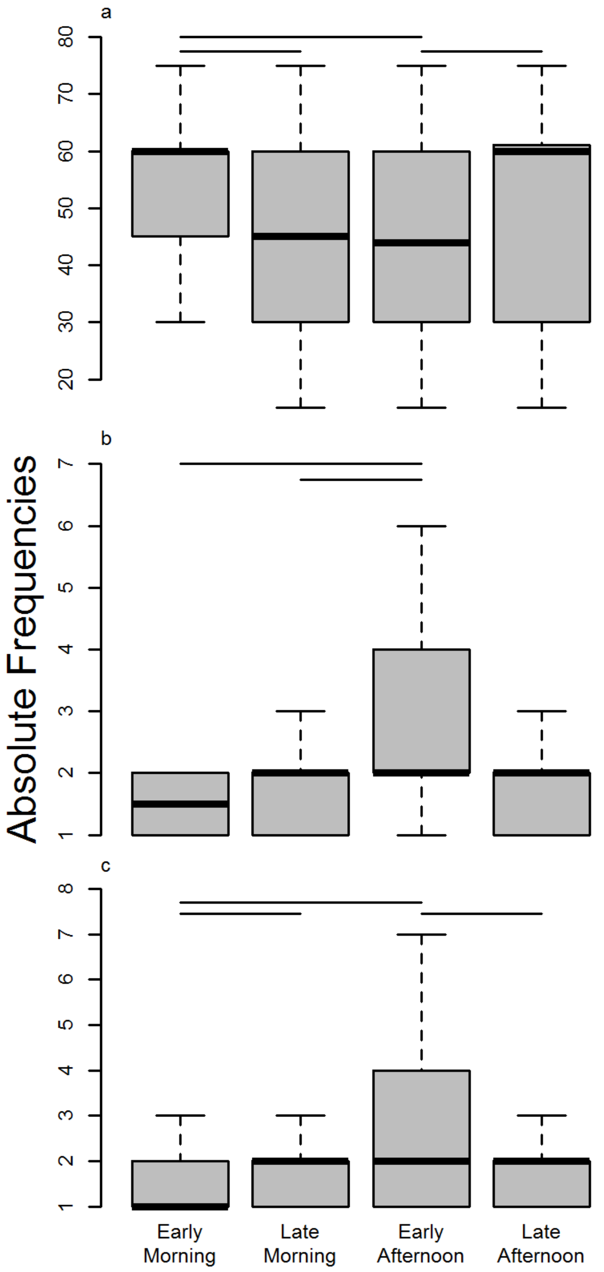

Figure 2. The absolute frequencies of movements displayed by fledglings of Red-footed Boobies with post-flight capacity at the nest site and across sampling stages among the shifts: Early morning = 06:00 to 09:00 h; Late morning = 09:00 to 12:00 h; Early afternoon = 12:00 to 15: 00 h; Late afternoon = 15:00 to 18:00 h. a) Frequency of fledgling presence at the nest; b) Frequency of arrival at the nest site by fledglings; c) Frequency of departure from the nest site by fledglings. The horizontal lines above the bars indicate significant probability value at $p \leqslant 0.05$ among the shifts.

The highest frequencies of fledgling presence at the nest site were recorded during the early morning and late afternoon, supporting the conclusion that they are synchronizing their foraging behavior with that of adults (Figure 2a). Additionally, Le Corre & Jouventin (1997) suggested that adult Red-footed Boobies delay their return to the nest colony in order to avoid attacks by pirating frigatebirds. We recorded the greatest number of encounters with frigatebirds, along with various other activities related to feeding, during the late afternoon shift (Figure 1). As adults tend to delay their return to the nest in order to avoid the attack by frigatebirds (Le Corre & Jouventin 1997), the fledglings have until late afternoon to return to the nest with a lower risk of losing their food for neighbor fledgling. In our data there was a higher frequency of arrival at the nest and departure from the nest by fledglings during the early afternoon shift when compared to the other shifts, characterizing a greater movement of the fledglings in the area, followed by the higher frequency of the fledglings present in the nest during the last shift of the day, probably anticipating the return of their parents.

Fledglings with the ability to fly would sometimes land on and roost in neighboring nests, apparently waiting for the adults to return. It seems that this strategy is advantageous because it allows the youngster to potentially acquire additional food resources and still monitor its own nest for the arrival of its parents. The end of parental care in Red-footed Boobies is directly related to decreasing the amount of food provided by the parents to their current offspring (Guo *et al*. 2010). This is a critical time during development and emancipation from caregivers, when fledgling demand for food is high and they must seek other means of acquiring sustenance (Yoda *et al*. 2007, Guo *et al*. 2010). These factors, coupled with the demands of achieving skilled flight capacity and the endurance that is necessary to forage for widely dispersed resources (Yoda *et al*. 2007, Kohno & Yoda 2011), favor the emergence of strategies that maximize the utilization of provisions that can be acquired directly from adults. The observations reported here indicate that Red-footed Booby fledglings may maximize their acquisition of available food resources by occupying neighboring nests when they are empty, or at least until the resident offspring returns. With this strategy, young birds increasing emancipation from parental care do not have to rely exclusively on the development of their own foraging capacity, by simply taking advantage of opportunities to solicit food from neighboring adults. It is important to note that Yoda *et al*. (2007) and Kohno & Yoda (2011) only focused the development of flight and diving capacity in boobies and we still have a very limited understanding of foraging efficiency and success in these birds.

In some avian species, parents are not able to identify their own offspring, and can only recognize the location of the nest, thus delivering food to any young bird that may be present (Varpe *et al*. 2004, Riou *et al*. 2012). In some cases, offspring may have certain physical characteristics that serve as cues for determining the intensity of parental effort (Wagner *et al*. 2013). Though we do not have sufficient evidence to confirm that adult Red-footed Boobies are unable to distinguish their own offspring from neighboring offspring, the documentation of alloparental feeding behavior by Lecomte *et al*. (2006) and Biaulieu *et al*. (2009), also supports this hypothesis.

In the current study we did not observe any fledglings successfully acquire supplementary food from neighboring adults, which may be an effect of the low density of nests during the study period, since the data were collected after the reproductive peak described for this species in the study area (Schulz-Neto 2004). It is likely that increased density, resulting in a greater proximity of nests, favors greater interaction between fledglings from neighboring nests. Guo *et al*. (2010) report having observed a young Red-footed Booby being provisioned by the parent of another individual that had died. According to the authors, the need for this species to make long foraging trips justifies the low rate of food delivery to offspring, putting additional selective pressure on the development of alternative food acquisition strategies in fledglings.

We conclude that non-detectable differences in behavioral frequencies of fledglings of Red-footed Boobies between the two phases of development observed in this study suggest that these birds have already reached a degree of maturity although with limited independence, requiring food supply from their parents, as seen in Guo *et al*. (2010). However, the occurrence of agonism between the fledglings, which was recorded when they are able to fly, strengthens the argument of decreasing the supply of food from parents to offspring in this advanced stage of development (Yoda *et al*. 2007, Guo *et al*. 2010). Further studies related to this stage of development and transition to independence of the fledglings can bring light over the strategies used by them to increase food acquisition during the period in which they are still learning to pursue their own resources in the open sea.

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