Cannibalism by Brown Booby (Sula leucogaster) at a small tropical archipelago

Felipe Machado Neves1, Patrícia Luciano Mancini1,2,3, Fernanda Pinto Marques1,2, Guilherme Tavares Nunes1,2 and Leandro Bugoni1,2,4

1 Waterbirds and Sea Turtles Laboratory, Institute of Biological Sciences, Universidade Federal do Rio Grande - FURG, CP 474, CEP 96203-900, Rio Grande, RS, Brazil.
2 Graduate Program in Biological Oceanography, Universidade Federal do Rio Grande - FURG, CP 474, CEP 96203-900, Rio Grande, RS, Brazil.
3 Current address: Seção de Aves, Museu de Zoologia da Universidade de São Paulo, CP 42694, CEP 04263-000, São Paulo, SP, Brazil.
4 Corresponding author: lbugoni@pq.cnpq.br

ABSTRACT: Cannibalism is the total or partial consumption of a conspecific’s body or eggs, and it has been reported for many bird taxa, particularly carnivorous, colonial species, and those species that ingest fragmented prey. Here we report cannibalism by Brown Booby (Sula leucogaster) at Saint Peter and Saint Paul Archipelago, offshore Brazil. We discussed possible causes for this behavior such as opportunistic feeding, colony sanitation and space competition for nesting places.

KEY-WORDS: chick mortality, opportunistic feeding, Saint Peter and Saint Paul Archipelago, seabirds, Sulidae.

INTRODUCTION

Direct cannibalism refers to the consumption of a living conspecific or its eggs (Stanback & Koenig 1992) and indirect cannibalism refers to scavenging on a conspecific whose death was due to other causes, including the action of predators (Riehl 2006). Cannibalism occurs in a wide range of animal taxa, from Protozoa to mammals, and has been reported for nearly every major vertebrate group, but it is infrequent in most species in which it occurs (Stanback & Koenig 1992, Pfennig 1997). Cannibalism in birds occurs primarily in species that are carnivorous, colonial, and that feed on fragments of prey rather than the whole prey (Stanback & Koenig 1992). Therefore, among wild birds, raptors and seabirds are the groups more prone to cannibalism (Stanback & Koenig 1992, Markham & Watts 2007, Andrew & Munro 2008). Among seabirds, cannibalism has been reported in gulls, pelicans, terns, frigatebirds and boobies (Stanback & Koenig 1992, Humphries et al. 2006, Gubiani et al. 2012, Hayward et al. 2014).

The Brown Booby (Sula leucogaster) is the most widely distributed Sulidae species, occurring in tropical and subtropical seas around the world (Nelson 2005). Typically, Brown Boobies capture fish and squids by plunge-diving (Harrison et al. 1983, Naves et al. 2002), but also feed on fishery discards (Krul 2004). The Brown Booby is monogamous and usually lays two eggs. Similarly to some other Sulidae species, the Brown Booby shows obligate siblicide (Anderson 1990, Drummond 2001, Nelson 2005, but see Tershy et al. 2000). Only one chick fledges, either because the parents only feed one chick or because the first-hatched chick or the parents eventually ejects the younger chick from the nest. Here we provide evidence for direct and indirect cannibalism involving chicks and adults Brown Booby at Saint Peter and Saint Paul Archipelago (SPSPA breeding colony), offshore Brazil.

METHODS

Study Area

The SPSPA (00°55’10”N, 29°20’33”W) is about 1,100 km from the Northeastern mainland Brazilian coast. It originates from a Meso-Atlantic elevation based at 4,000 m depth and comprises 15 rocky islets covering an area of 17,500 m². Belmonte is the largest islet, about 100 m long, 50 m wide and the highest point of the archipelago is 18 m above sea level (Vaske-Jr et al. 2010). SPSPA is located in an oligotrophic area, directly influenced by the South Equatorial Current, flowing from east to west, and the Equatorial Undercurrent, which flows in the opposite direction and with core located about 80 m depth (Travassos et al. 1999). Approximately 580
Brown Boobies, 390 Brown Noddies (Anous stolidus) and 320 Black Noddies (A. minutus) breed in SPSPA (Both & Freitas 2004, Neves et al. 2013). The number of Brown Boobies is fairly constant year round and about 90% of these birds occur on Belmonte Islet, in a dense monospecific colony (Barbosa-Filho & Vooren 2010) while other islets are used mainly for roosting by this species (Naves et al. 2002, Both & Freitas 2004, Barbosa-Filho & Vooren 2010). Flyingfishes are key prey species for tuna, sharks and seabirds (Mancini & Bugoni 2014), while the abundant fishery resources are explored by a commercial fishery of regional importance based on the mainland (Vaske-Jr et al. 2005).

Observations
Research expeditions to SPSPA occurred in August 2011, January 2012, May-June 2014 and July 2015. Initially, we observed two Brown Booby pairs (including the parents of a dead chick) pecking rapidly and repeatedly on the dead nestling, although we did not notice consumption of the body. This aggressive behavior suggested that cannibalism could occur at this colony and, therefore, a behavioral experiment was developed to study the occurrence of cannibalism. We collected fresh chick carcasses resulting from natural mortality in their original nests or close to them. To assess propensity for cannibalism, we carried out seven experimental trials. We placed a dead chick next to paired Brown Boobies defending a nest site without eggs or chicks. We carried out experimental trials opportunistically whenever a dead chick was found, and observed and recorded with photography and video the reaction of the receiving pairs towards the dead chick. We paid particular attention to whether receiving birds swallowed the chick carcass, and the age and sex of cannibals. We determined sex of adults by vocalizations or the colors of the head, skin or bill, and determined age by plumage colors (Harrison 1983). Finally, we estimated the age of the dead chicks following Barbosa-Filho & Vooren (2010), and then used age to estimate body mass of ingested chicks (Coelho et al. 2004).

RESULTS
Experimental Trials
Trial 1 (19 August 2011). We collected one 3-week old chick (~300 g) found dead close to its original nest and placed it on the ground, in front of a Brown Booby pair that was defending an empty nest. Both birds observed the chick for a few seconds. The male approached the chick and moved it closer to the female, which immediately swallowed the chick.

Trial 2 (19 August 2011). We found a dead 3-week old chick (~300 g) and placed it on the ground next to a pair, different from the previous pair. The pair soon approached the chick and the female swallowed it (Figure 1).
Trial 3 (11 January 2012). We observed a breeding male Brown Booby at 10:10 h (GMT-2), close to its own 4-week old dead chick (~400 g). This male continually moved soil, small stones, and the chick around the nest in a manner similar to nest-building behavior. With the chick out of the nest, this behavior continued and a small hole was dug in the ground. By 12:00 h, the pair was in the nest and the dead chick was at the same place, close to the nest. Shortly after, we removed the chick from the vicinity of the pair. The parents became restless, as did the neighboring boobies.

Trial 4 (11 January 2012). We placed the dead chick (the same specimen used for trial 3) in a nearby nest occupied by a pair without chick or egg. The receiving pair began to peck at the chick as soon as they perceived its presence. A nearby nearly-fledged, flightless chick got involved and exhibited aggressive behavior towards the receiving pair and other birds around, including the parents of the dead chick. The nearly-fledged chick persistently attempted to swallow the dead chick for about 10 min (Figure 2), but was unsuccessful due to its small size relative to the dead chick and its gape width limitation. When the nearly-fledged chick finally stopped its attempts, the juvenile’s mother immediately grabbed the dead chick and tried to swallow it for about 1 min, again unsuccessful due to gape limitation. The dead chick was then left on the ground.

Trial 5 (11 January 2012). We moved the dead chick (from trials 3 and 4) to another nest occupied by a pair without chick or egg. Both adults pecked and shook the chick vigorously for 2 min, the female acting more aggressively, and then set it aside without trying to swallow it.

Trial 6 (15 May 2014). We placed an adult Brown Booby carcass on the other side of booby nests, away from birds. About 2 min later a female grabbed the carcass and tried to swallow it repeatedly, but was unsuccessful due to gape limitation. She left the carcass on the ground and a wave washed it away from the colony.

Trial 7 (31 May 2014). We found a dead chick (~300 g) and placed it near a nest occupied by a pair without chick or egg. A female pecked at the chick and tried to swallow it, but was unsuccessful due to gape limitation. Male and female continued pecking the dead nestling, but lost interest over time.

Apart from the trials explained above, during a 1-month expedition, two spontaneous cannibalistic events were recorded. On 20 July 2015, a female pushed out their younger nestling (3 days old; <100 g) and promptly, an adjacent breeding pair caught the still alive chick, and the male swallowed it (Figure 3). On 27 July 2015, a breeding male caught and swallowed a 1-week old nestling (<100 g) from the adjacent nest, while researchers were sampling the adult attending the nest, which did not last more than 5 minutes.

Overall, from seven trials and two spontaneous observations, we report seven cannibalistic events by Brown Booby individuals at SPSPA.

FIGURE 2. A nearly-fledged Brown Booby (*Sula leucogaster*) attempting to swallow a dead chick from an adjacent nest at Saint Peter and Saint Paul Archipelago, Brazil. (Photo: F. P. Marques)
Cannibalism in sulid species was recorded a single time in the Nazca Booby (Sula granti) in more than 15 years of research at Galapagos Islands (Humphries et al. 2006). However, Brown Booby cannibalism at SPSPA was reported previously in two unpublished sources. The first report was part of a Ph.D. thesis, which included a Brown Booby diet study at SPSPA and one chick was observed in a female regurgitate, sampled between 1999-2001 (Kohlrausch 2003). The second report was from expedition diaries (Expedition No. 164, and report by C.J.A. Costa-Jr., A. Cavalcante and C.M. Vooren), which described a female with a broken wing that ate a live chick when it was ejected from the nest by its parents in August 2004. Thus, cannibalistic behavior had been previously observed at our study site, apparently under natural circumstances, i.e. without an intentional delivery to potential cannibals as in our trials.

Many hypotheses have been suggested to explain cannibalism in birds. In the broken winged female case, cannibalism could have occurred due to acute food limitation (Ingram 1959, Stanback & Koenig 1992, Nishimura 2010), because the female was flightless and food deprived. Cannibalism has been associated with food shortage in other species, such as the Long-tailed Jaeger (Stercorarius longicaudus) (Vooren & Chiaradia 1989), the Australian Pelican (Pelecanus conspicillatus), the Australian White Ibis (Threskiornis molucca) (Andrew & Munro 2008), the Peruvian Pelican (P. thagus) (Daigre et al. 2012), and the Socotra Cormorant (Phalacrocorax nigrogularis) (Gubiani et al. 2012). In our observations (trials 1, 2, 4, 6, 7, and the two events of spontaneous cannibalism), as well as in the case reported by Kohlrausch (2003), in which Brown Booby chicks were consumed or there was attempted consumption, a possible explanation could be an opportunistic feeding behavior by females to restore energy during breeding. In seabirds, including sulids, males and females generally share breeding duties equally (Nelson 2005, Lormee et al. 2005, Weimerskirch et al. 2006). However, at SPSPA, female Brown Boobies are mostly responsible for feeding chicks (80% of the time, compared to males, Kohlrausch 2003). In the SPSPA, the Brown Booby breeds throughout the year and there has been no report of yearly variation in the occurrence of breeding (Both & Freitas 2001, Barbosa-Filho & Vooren 2010). Furthermore, in SPSPA, seabirds and marine pelagic fish rely on the same prey species (flyingfish), but the overlap in their trophic niches was limited, most likely due to an overabundant food resource (Mancini & Bugoni 2014).

The availability of food for seabirds at the SPSPA is probably constant and predictable through the year (Barbosa-Filho & Vooren 2010). SPSPA slows the Equatorial Undercurrent, increasing residence time of nutrients around the archipelago and generating subsurface vortices (Araujo & Cintra 2009). This process increases local primary productivity and allows a great abundance of flyingfish, large pelagic fishes and intense fisheries around the SPSPA (Vaske-Jr et al. 2003, 2008, Viana et al. 2012). Thus, food shortage does not seem to be driving cannibalistic behavior. The ‘icebox hypothesis’ (Alexander 1974), alternatively, considers that a marginal offspring is a potential feeding resource and that its consumption confers breeding advantage to the parents (Ingram 1959). Filial cannibalism (consumption of all or part of the young by the parents) may be an adaptive strategy where energetic requirements trigger cannibalism (Klug & Bonsall 2007). However, cannibalism seems to
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Contribute only a marginal increment to the breeding success of the Nazca Booby, and Humphries et al. (2006) did not observe family members consuming chicks because the similar size of siblings precludes such behavior. At SPSPA, most cannibalistic birds were females, and in one instance (trial 1), the male offered the dead chick to the female, in line with the food deprivation hypothesis, which could help offset energetic costs of egg production. The exceptions were the two spontaneous cannibalism events recorded in July 2015, when males swallowed chicks, which suggests that this hypothesis does not explain all cannibalistic events at SPSPA.

Furthermore, cannibalism may be a density-dependent behavior (Fox 1975, Nishimura 2010). At high nest densities, egg cannibalism and social stress increase in gulls (Burger 1980, Brouwer & Spaans 1994), and disputes over territories are frequent in booby colonies (Alves et al. 2004, Nelson 2005). The SPSPA Brown Booby population increased from 334 birds in 2000-2001 (Barbosa-Filho & Vooren 2010) to 588 birds in 2011-2014 (Neves et al. 2013, Mancini et al. unpublished data) and no emigration has been documented (Barbosa-Filho & Vooren 2010). In this colony there is an average distance between nests of 1 m, while in the Rocas Atoll, northeastern Brazil, for instance, nests are 11 m apart on average (Kohlrausch 2003). Furthermore, average nest diameter of SPSPA is ~20% smaller than Rocas Atoll nests (Kohlrausch 2003). Some additional observations of the authors on the Brown Boobies at SPSPA also suggest space limitation. Fights over territory in the nest surroundings are intense and common, resulting in injured adults or chick death. Furthermore, boobies frequently establish nests in low, marginal areas, close to the area of wave action, i.e., low quality areas with reduced breeding success. In both spontaneous events reported here, cannibalized chicks belonged to nests adjacent to canals. All this suggests that cannibalism could be a density-dependent behavior, and eating chicks from adjacent nests would be a way of eliminating adjacent nests.

On the other hand, an alternative hypothesis is that cannibalism could have a colony sanitation role. The ingestion of nesting fecal sacs by adult birds in nests, as well as the removal of egg shells, feces and dead nestlings, is a well-known phenomenon (Blair 1941, Kirkpatrick et al. 2009). This behavior could be important in partially closed nests, and could be potentially essential in crowded places as at the SPSPA, where the only potential scavenger is the crab (Grapsus grapsus). However, as far as we know, cannibalism in seabirds has not been suggested as playing a role in sanitation of colonies, which requires further investigation.

Finally, constant human presence in the archipelago since 1998, when the “ProArquipélago Program” was established by the Brazilian Navy, may be influencing this behavior. Since then, the island has been permanently inhabited by small groups of researchers and mariners (usually four). Additionally, researchers, sailors and fishermen often feed boobies left-over fish parts, and individuals with a propensity for cannibalistic behavior may have interpreted the dead chicks thrown close to the nests (our trials) as a food offer by humans, despite this does not explain the spontaneous cannibalism events reported. In summary, explanations for the natural cannibalism reported previously, as well as our ‘unnatural’ trials, which result in cannibalistic attempts, remain elusive, and further experimental studies should be carried out to address why Brown Boobies from this area differ from sulids elsewhere.

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