Segregation in Diet between Black Noddy (*Anous minutus*) and Brown Noddy (*A. stolidus*) from the Southern Lagoon of New Caledonia[1]

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Abstract: The Black Noddy (*Anous minutus*) and the Brown Noddy (*A. stolidus*) occur sympatrically in the Southern Lagoon of New Caledonia, breeding on islets located at the edge of a wide, productive coral-reef lagoon next to oceanic waters enriched by a seasonal upwelling. The diets of the two species were determined from regurgitations from birds nesting at Kouaré Islet during two consecutive breeding seasons (2002/2003 and 2003/2004) and compared. The average prey load in the Brown Noddy was heavier than that in the Black Noddy, as expected from its larger body size and from a predicted longer foraging distance. Fish prey dominated the diet of both species (100% and 81.8% biomass in Black and Brown Noddies, respectively); the remainder consisted of squid. Black Noddy ate small pelagic fishes inhabiting the reef and the lagoon, mainly round herrings (*Spratelloides* spp.), and Brown Noddy mainly preyed on offshore species including buccaneer anchovy (*Encrasicholina punctifer*) and larger pelagic fishes (Exocoetidae) and squids. The segregation in diet between Black and Brown Noddies in New Caledonia thus indicated spatial segregation in foraging zones (i.e., inshore versus offshore, respectively), which was more pronounced than previously reported for other sites where the two species co-occur.

The Black Noddy (*Anous minutus*) and the Brown Noddy (*A. stolidus*) have tropical distributions; the latter is pantropical. Much of their ranges overlap, except in the Indian Ocean, where the Black Noddy is replaced by its slightly smaller sister-species, the Lesser Noddy (*A. tenuirostris*) (Higgins and Davies 1996, Bridge et al. 2005). Noddies depend for feeding on large marine predators, particularly tunas: tunas prey on schools of small pelagic fishes by concentrating them toward the surface before going through the school to catch them (Ashmole 1962, Hulsman 1988). Noddies catch their prey either by dipping or, though more rarely, by surface plunging (Chardine and Morris 1996, Gauger 1999). Brown Noddy may also catch fishes in the air (Ashmole 1971).

Brown and either Black or Lesser Noddies breed in sympatry in a number of localities, although usually one species largely outnumbers the other (Dorward and Ashmole 1963, Ashmole and Ashmole 1967, Harrison et al. 1983, Surman and Wooller 2003, Ramos et al. 2006). In the Southern Lagoon of New Caledonia (Southwest Pacific Ocean) (Figure 1), the Black Noddy (*A. minutus minutus*) outnumbers the Brown Noddy (*A. stolidus pileatus*) by ca. 60,000 pairs to ca. 1,000 pairs (Pandolfi-Benoit and Bretagnolle 2002). Although the Southern Lagoon comprises more

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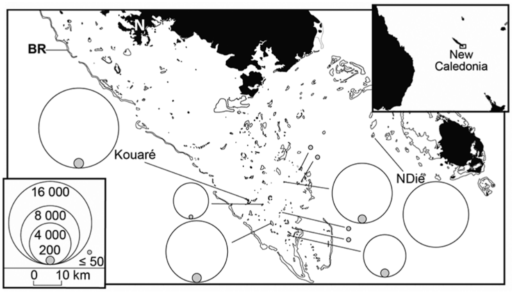

Figure 1. Map of the Southern Lagoon of New Caledonia showing the location and abundance of nesting colonies of Black Noddy (open circles) and Brown Noddy (gray-filled circles). Size of a circle is proportional to the number of nests, counted during the survey reported here (all islets except Ndié), or to the number of breeding pairs (on Ndié islet [Pandolfi-Benoit and Bretagnolle 2002]); *solid black:* landmass; *thin lines* delineate coral reefs; *N:* Nouméa city; *BR:* barrier reef delimiting the Southern Lagoon. *Left inset:* proportionality of circle size to population size. *Right inset:* location of New Caledonia in the southwestern Pacific, with box indicating large view.

than 55 islets, the Black Noddy breeds on only six of them, five of which are also nesting sites for the Brown Noddy (Figure 1).

We analyzed the diet of Black and Brown Noddies breeding in sympatry and in synchrony, choosing an islet of the Southern Lagoon of New Caledonia as the study site. Several predictions on prey composition can be made on the basis of morphological differences between the two species. Although bill length is similar in Black and Brown Noddies (Higgins and Davies 1996), it is thicker in the Brown Noddy, enabling it to grab larger prey than the Black Noddy (Ashmole and Ashmole 1967, Harrison 1990). Therefore, one expects prey size to be larger in Brown Noddy. This in turn is expected to have an effect on prey composition. Furthermore, because of its larger size (the Brown Noddy is almost twice as heavy as the Black Noddy), the Brown Noddy should be able to carry a heavier load than the Black Noddy. Also, all other things being equal, the larger body of the Brown Noddy implies higher energy needs, making it likely to exploit a wider range (Mace and Harvey 1983) than the Black Noddy. Morphological differences between the two species thus allow us to predict differences in both prey size, prey load, and foraging range.

MATERIALS AND METHODS

Study Area

Fieldwork was done at Kouaré Islet (22° 47′ S, 166° 48′ E), a 7.4 ha coral cay located in the Southern Lagoon of New Caledonia, 43.2 km from the main island and 6.3 km from the barrier reef (Figure 1). The Southern Lagoon has the shape of a funnel, is ca. 100 km long and ca. 40 km wide, and is oriented from the southeast to the northwest, which is approximately the direction of the trade winds; it has a mean depth of 17.5 m (Chevillotte et al. 2005). The barrier reef that surrounds mainland New Caledonia isolates the lagoon from the Coral Sea (Figure 1). Oceanic waters immediately off the barrier reef are subject to strong cooling (by 5°C) related to an intense wind-driven, seasonal (from October to April) coastal upwelling (Alory et al. 2006, Marchesiello et al. 2010). Enhanced northward wind stress and saltier and colder waters have been noticed during El Niño years (Alory et al. 2006). This may have consequences on the productivity of the oceanic waters off the Southern Lagoon because the concentration of chlorophyll *a* increases during coastal upwelling events (Alory et al. 2006).

Prey Sampling and Analysis

Breeding noddies were studied during two successive breeding seasons: 27 days (three periods of 9 days each) between 30 December 2002 and 18 February 2003 (“2002/2003”), and 28 days (two periods of 12 and 11 days, and five short stays of 1 day each) between 20 November 2003 and 17 February 2004 (“2003/2004”). The 2002/2003 season was characterized by moderate El Niño conditions, whereas the 2003/2004 season was neutral (Singh et al. 2011). Prey samples came directly from adults and fledglings caught in the colony with a fish landing net. Without further manipulation, the individuals regurgitated their meal, after which they were released without being fed in compensation.

Regurgitated items were collected directly in a sampling vial or scooped from the nest using a spoon and preserved in 95% ethanol immediately afterward. Sixty-two regurgitation samples were collected from Black Noddy in 2002/2003 and 23 in 2003/2004; for Brown Noddy, sample sizes were 44 in 2002/2003 and 5 in 2003/2004. The differences in sample size according to year reflect only sampling effort. Regurgitations were subsequently washed with 95% ethanol using a wash bottle, and the prey items were sorted by prey type.

Entire prey items were distinguished from body portions or sections, and undigested prey items were distinguished from partially digested ones. "Intact" means the prey was regurgitated whole, showed no apparent injury and showed no sign of digestion; "quasi-intact" means the prey was also regurgitated whole and undigested but showing cuts, bites, punctures, or other injuries. We also included in the latter category prey items that consisted of an entire undigested fish but whose head was smashed mechanically. Other prey items were partial (for example, a decapitated fish or a fish lacking its tail). Degraded skin, exposed and chemically degraded muscle, or exposed and chemically degraded bone were considered as evidence of digestion. A higher percentage of digested items in a regurgitation was assumed to reflect a longer foraging trip.

Prey items consisted of either fishes or squids. Fishes were identified to family, sometimes to genus, and in some cases to species (Appendix) according to the identification keys and descriptions given in Carpenter and Niem (1999, 2001). Fish prey items that lacked key morphological parts were compared with those that were identifiable to species in the same regurgitation or in samples collected on the same day from other individuals in the colony or to reference collections of specimens of small pelagic fishes from the Southern Lagoon of New Caledonia preserved in alcohol at the IRD laboratory in Nouméa. All prey items in a regurgitation were measured individually on sheets of graph paper. Drained prey items in a regurgitation were then grouped by species, or genus, or family (whenever possible), counted, and weighed to provide prey biomass. Advanced digested remains forming the liquid phase of a regurgitation, when present, were eliminated by washing before sorting, hence not weighed. All regurgitation samples have been deposited at IRD laboratories in Nouméa.

Two-tailed Student's t test for independent distributions was used to compare the distributions of average length and weight of prey item between the two noddy species. Two-way analysis of variance (ANOVA) was used to test the effect of season and noddy species on the weight of regurgitated prey. The null hypothesis that prey species composition in noddies was the same between seasons was tested by a χ^2 test of homogeneity

RESULTS

Intact or quasi-intact prey represented 6% and 1% of prey items in Black and Brown Noddies, respectively. A proportion of prey items showed injuries (punctures, bites, cuts, gashes) attributable to predators with sharp cutting beaks or with small, conical teeth. Partial prey items included decapitated fishes, fishes lacking their tail, and body sections presenting sharply cut edges. Some other prey items consisted of entire fish with mechanically smashed heads. Among the body sections recovered were half fishes, single heads, and single tails. For example, one regurgitation of a Black Noddy contained six intact *Spratelloides delicatulus* and a single tail of the same fish species; another contained six decapitated *S. gracilis* and three tails of the same fish species; one regurgitation of a Brown Noddy exclusively contained squids including three intact individuals, one mantle, and a portion of the mantle of another individual; another contained a single Exocoetidae. In total, mechanical injuries before ingestion by noddies were inferred for 36.7% and 36.1% of the regurgitated prey in, respectively, Black and Brown Noddies. Up to 19% recovered prey items showed evidence of partial digestion in Black Noddy, and this figure reached 47% for Brown Noddy.

Prey items regurgitated by Black Noddy, including both intact prey and prey fragments, did not differ significantly from those of Brown Noddy in average length (22.3 ± 11.5 mm and 21.8 ± 14.5 mm, respectively) ($t = 0.778$, df = 1596, $P = .469$). However, the average weight of a prey item was significantly less for Black Noddy, as compared with Brown Noddy (0.44 ± 0.37 g versus 1.89 ± 2.56 g, respectively) ($t = 5.936$, df = 190, $P < .001$). Upper extremes reached 66 mm and 2.8 g [an intact buccaneer anchovy (*Encrasicholina punctifer*)] in Black Noddy versus 101 mm and 10.6 g (the posterior part of an Exocoetidae) in Brown Noddy. The average weight of the total prey items in a regurgitation was 3.9 ± 3.1 g in Black Noddy (range 0.3–13.3 g), which was significantly less than in Brown Noddy (6.8 ± 4.6 g, range 0.1–16.7 g) ($F = 12.8$; df = 1, 128; $P < .001$).

Fish prey dominated the diet of both species (100% and 81.8% biomass in Black and Brown Noddies, respectively); the remainder consisted of squid. Six fish families were represented in the prey items of Black Noddy and Brown Noddy, three of which (Carangidae, Clupeidae, and Engraulididae) were found in the regurgitations of both species. Differences in diet were apparent (Figure 2), with the most abundant prey in regurgitations of Black Noddy being silver-striped round herring (*Spratelloides gracilis*), which accounted for 74.5% of prey items (Appendix). This species was totally absent from identifiable regurgitations from Brown Noddy. Conversely, the family Engraulididae (*Enchrasicholina*) was poorly represented in the diet of the Black Noddy (7% of prey items) but was the most abundant prey in the Brown Noddy diet (73% of prey items). Both species preyed marginally on delicate round herring (*S. delicatulus*), which on the average represented 14% and 15% of prey items for Black and Brown Noddies, respectively. Only Black Noddy preyed, albeit marginally, on Atherinidae (2% of prey items), and only Brown Noddy preyed on Exocoetidae (5% of prey items) and squids (4% of prey items).

We checked whether the prey species composition varied between the two seasons. For example, silver-striped round herring, the main prey of the Black Noddy, represented 65% of its total prey items in 2002/2003 and reached 84% in 2003/2004, and anchovies, which represented 14% of its prey items in 2002/2003, were absent in 2003/2004 (Appendix). However, taking into account the number of regurgitations containing a given prey species, these differences were not significant ($\chi^2 = 3.6$, df = 3, $P > .30$).

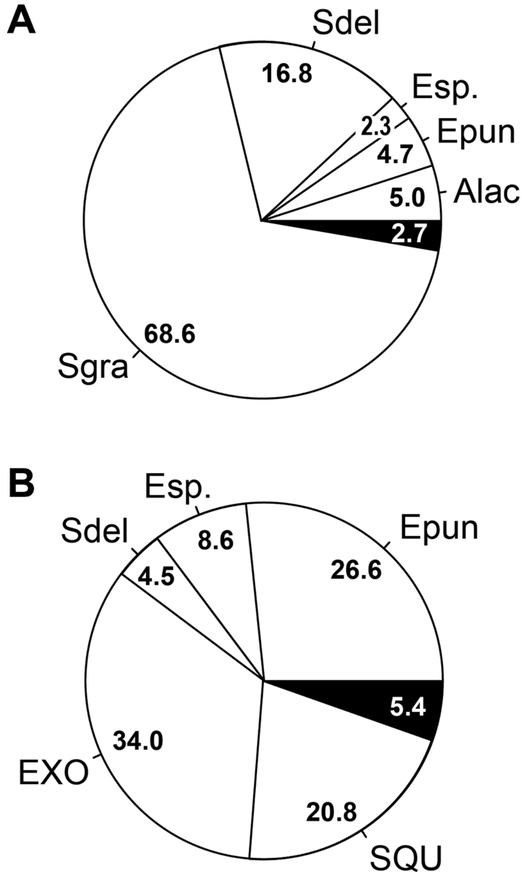

FIGURE 2. Prey composition (expressed as percentage of total prey biomass, given inside each portion of the diagram) for two noddy species nesting on Kouaré Islet, New Caledonia, from pooled data from two consecutive breeding seasons (austral summers 2002/2003 and 2003/2004). Alac, *Atherinomorus lacunosus;* Epun, *Encrasicholina punctifer;* Esp., *Encrasicholina* sp.; EXO, Exocoetidae; Sdel, *Spratelloides delicatulus;* Sgra, *S. gracilis;* SQU, squid. The other fish prey species and unidentified fish prey were lumped into the black portion of each pie diagram. (*A*) Black Noddy ($n = 85$ regurgitation contents); (*B*) Brown Noddy ($n = 49$).

DISCUSSION

Basic knowledge of diet and foraging habitat is relevant to the management of seabirds in a conservation perspective. The results reported here demonstrated differences in diet composition between Black and Brown Noddies nesting in the Southern Lagoon of New Caledonia. As explained in the following, these differences may in part reflect morphological differences between the two seabirds. They also indicate different foraging habitats.

The observations reported here confirm that Black and Brown Noddies partly if not largely rely on other predators to collect their prey (e.g., Harrison et al. 1983). This may not only include predatory fishes as previously reported, but also other seabirds. The noddies would have picked up these prey items on the surface after they had been disabled by seabird or fish predators.

The weight of a total regurgitation was on the average higher for the Brown Noddy than it was for the Black Noddy and reached slightly higher maximum values. Similar observations have been made in Hawai'i (Harrison et al. 1983) and in the central Atlantic (Coelho Naves et al. 2002). These observations agree with the prediction that the Brown Noddy should be able to carry a heavier load than the Black Noddy because of its larger size. In New Caledonia, the maximum prey load in the Black Noddy nevertheless was heavier than the single Exocoetidae or squid items regurgitated by the Brown Noddy, suggesting that the absence of Exocoetidae and squids in the diet of the Black Noddy was not due to the smaller body size of the Black Noddy, relative to the Brown Noddy. Still, this difference might be caused by the capacity of the Brown Noddy to capture or ingest single larger prey than the Black Noddy.

The absence in the diet of the Brown Noddy of silver-striped round herring, the main prey of the Black Noddy, cannot be explained by morphological differences between the two noddy species because of the relatively small size of the silver-striped round herring. Therefore, its absence in the Brown Noddy diet likely reflects its absence in the latter's foraging habitat. Both round herring species are considered to be inshore schooling species, characteristic of the reef and lagoon habitats (Conand 1988, Froese and Pauly 2005). Similarly, the rarity or, perhaps, the absence of buccaneer anchovy in the diet of the Black Noddy, when this prey species accounted for a substantial part of the diet of the Brown Noddy, is unlikely to be a direct consequence of morphological differences between the two noddy species. The buccaneer anchovy is considered to be an oceanic species (Froese and Pauly 2005), and of all anchovy species present in New Caledonia it is the only one to occur in dense schools far offshore (Conand 1988). Most members of the Exocoetidae family, which were exclusive to the diet of the Brown Noddy, are pelagic fishes inhabiting the open ocean and neritic surface waters (Randall et al. 1997, Parin 2001). Exocoetidae are rarely observed inside the Southern Lagoon of New Caledonia (P.B., pers. obs.); they are absent from the extensive collections of pelagic fishes from the coastal lagoons around New Caledonia (Conand 1988). Prey composition thus provides information on the foraging habitats of the two noddy species in New Caledonia. It indicates that the Black Noddy forages inshore or close to the reef front, and the Brown Noddy ventures farther offshore, with little, if any, spatial overlap. These conclusions are indirectly supported by the higher proportion of digested prey items in the Brown Noddy diet relative to the Black Noddy, which suggests a longer foraging trip.

It has been previously reported that the Brown Noddy tends to forage in more pelagic waters than Black or Lesser Noddies (Ashmole and Ashmole 1967, Harrison et al. 1983, Tarburton 1987, Seki and Harrison 1989, Surman and Wooller 2003). However, the foraging ranges of Brown and Lesser Noddies largely overlap, and they have a similar spectrum of preys (eastern Indian Ocean [Surman and Wooller 2003]). So do, reportedly, Black and Brown Noddies (Hawaiian archipelago [Harrison et al. 1983, Keller et al. 2009]; central Atlantic [Coelho Naves et al. 2002]). The inshore versus offshore segregation in diet between Black and Brown Noddies from Kouaré Islet was much more pronounced than previously reported from other sites. We suggest that pronounced segregation in diet is possible in New Caledonia because of the variety of productive marine habitats immediately accessible to Black and Brown Noddies. These include a wide, productive inshore lagoon exploited by the Black Noddy, and oceanic waters affected by a seasonal upwelling, where the Brown Noddy was inferred to forage preferentially.

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Appendix

Prey Composition [Expressed as Percentages of Total Number of Prey Items (%Number) and Total Biomass of Prey (%Biomass)] for Black and Brown Noddies Nesting on Kouaré Islet, New Caledonia, for Two Consecutive Reproductive Seasons (Austral Summer 2002/2003, Austral Summer 2003/2004)

	Black Noddy						Brown Noddy					
	2002/2003			2003/2004			2002/2003			2003/2004		
Prey	n[a]	%Number	%Biomass	n[a]	%Number	%Biomass	n[a]	%Number	%Biomass	n[a]	%Number	%Biomass
Ambassidae												
Ambassis vachelli	1	0.3%	0.9%	—	—	—	—	—	—	—	—	—
Atherinidae												
Atherinomorus lacunosus	4	4.1%	6.1%	—	—	—	—	—	—	—	—	—
Undetermined	—	—	—	2	0.5%	0.8%	—	—	—	—	—	—
Carangidae												
Decapterus sp.	—	—	—	—	—	—	—	—	—	1	1.9%	12.4%
Undetermined	3	1.2%	1.3%	—	—	—	—	—	—	1	1.0%	0.2%
Clupeidae												
Spratelloides delicatulus	16	13.4%	17.6%	6	14.9%	13.1%	2	1.8%	1.0%	3	27.6%	28.6%
Spratelloides gracilis	45	65.3%	65.3%	17	84.0%	84.6%	—	—	—	—	—	—
Engraulididae												
Encrasicholina punctifer	4	5.3%	5.7%	—	—	—	19	59.8%	30.4%	—	—	—
Encrasicholina sp.	6	8.9%	2.8%	—	—	—	8	22.3%	9.0%	2	63.8%	5.7%
Exocoetidae	—	—	—	—	—	—	15	8.1%	37.1%	1	1.9%	12.7%
Gempylidae	—	—	—	—	—	—	1	0.7%	1.3%	—	—	—
Hemirhamphidae	—	—	—	1	0.3%	0.3%	—	—	—	—	—	—
Pomacanthidae	—	—	—	—	—	—	1	0.2%	0.6%	—	—	—
Unidentified fish remains	5	1.5%	0.4%	1	0.3%	1.2%	5	1.4%	2.3%	1	1.0%	1.2%
Squid	—	—	—	—	—	—	12	5.6%	18.2%	3	2.9%	39.1%
Total	(62)	662	279.8 g	(23)	388	58.2 g	(44)	443	277.6 g	(5)	105	40.2 g

[a] *n*, number of regurgitations containing the prey; in parentheses: total number of regurgitations.