Seasonal and inter-annual variation in the feeding ecology of a tropical oceanic seabird, the red-tailed tropicbird *Phaethon rubricauda*

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ABSTRACT: We studied seasonal and inter-annual variations in the diet, amount of food delivered to chicks, and body condition of chicks and adult red-tailed tropicbird at Europa Island (Mozambique Channel, Indian Ocean), during 3 consecutive seasons. The diet consisted of epipelagic fishes (13 families) and squid (3 families) totalling 32 taxa. Three families, the squid Ommastrephidae (mainly *Sthenoteuthis oualaniensis*) and the fishes Exocoetidae (flying-fish) and Coryphaenidae (dolphin-fish), accounted for 68% of the number of prey and 83% of the ingested biomass. There were considerable differences in size and mass of the prey items, dolphin fish being the largest and squid the smallest. There were important seasonal variations in diet. During chick-rearing, 41% of the mass of food delivered to chicks consisted of dolphin fish, whereas these fish represented only 2% of the mass of food during incubation. The squid were caught in similar proportion throughout the breeding season but were larger during chick rearing. We did not find any inter-annual variation in the diet of chicks, nor in the body condition of either fledglings or adults, suggesting that no major inter-annual changes in food availability occurred during the course of our study. However, there was some inter-annual variation in feeding frequency and body condition of chicks of less than 60 d. There were also significant day-to-day variations in the feeding frequency in one of the 3 seasons studied. This suggests that day-to-day variation in the marine environment or in foraging conditions may have short-term consequences in the food provisioning and body condition of growing chicks, but that these variations do not necessarily result in long-term (inter-annual) variations in diet and body condition of fledgling or adult red-tailed tropicbirds at Europa island. These results suggest that between 1995 and 1997, red-tailed tropicbirds of Europa relied on predictable and seasonal food resources when breeding.

KEY WORDS: Tropicbird · *Coryphaena* · *Sthenoteuthis oualaniensis* · Provisioning rate · Body condition · Diet · Indian Ocean

INTRODUCTION

Tropical seabirds live in a marine environment with fewer and less predictable variations than species living at higher latitudes (Ashmole 1971). Thus it is generally argued that the food available to tropical seabirds does not show important seasonal variations (within a year) but may vary among years in relation to unpredictable events like ENSO (El Niño Southern Oscillation), which can have important consequences on growth rate, breeding success or laying date of seabirds (Schreiber & Schreiber 1984, Valle et al. 1987, Cruz & Cruz 1990, Ramos et al. 2002). These specific conditions might lead first to non-seasonal or very protracted breeding periods and second to inter-annual variations in the feeding ecology and body condition of tropical seabirds. Although the breeding regimes of tropical seabirds have been studied at various places (e.g. Harris 1969, Schreiber &

Ashmole 1970, Morris & Chardine 1992), few studies focused on inter-annual variations in breeding parameters. Some studies conducted in the tropical Pacific Ocean (e.g. Ricklef et al. 1984, Schreiber 1994, Shea & Ricklefs 1996, Boersma 1998), and 1 in the tropical Indian Ocean (Ramos et al. 2002) have shown that inter-annual changes in population size, chick growth or breeding success were related to changes in the marine environment. However, no author studied inter-annual variations in diet, feeding frequency and body condition of chicks and breeding adults in the same population of a tropical seabird. In this paper, we investigated both seasonal and inter-annual variations of these parameters in a red-tailed tropicbird *Phaethon rubricauda* population, in order to test the generally accepted idea that tropical seabirds live in an environment with few seasonal variations but unpredictable inter-annual variations.

The red-tailed tropicbird is a long-lived seabird, widely distributed in the tropical regions of the Pacific and Indian Oceans (del Hoyo et al. 1992). In the western Indian Ocean, there are around 6000 pairs breeding at 6 localities (Diamond 1975, Feare 1984, Cooke & Randriamanindry 1996, Le Corre & Jouventin 1997). Europa Island (southern Mozambique Channel) holds the largest breeding population of the Indian Ocean (Le Corre & Jouventin 1997), corresponding to 60% of the western Indian Ocean population (ca. 3500 pairs). Although no detailed study has been conducted on the foraging behaviour of this species at sea, it is regarded as very oceanic, according to both observations at sea and duration of foraging trips when breeding (Diamond 1975, Schreiber & Clapp 1987). As the other 2 members of the Family Phaethontidae, the red-tailed tropicbird forages solitarily (Bailey 1968, Harrison et al. 1983) and is rarely associated with flocks of surface-feeding predatory fishes (Ashmole & Ashmole 1967, Au & Pitman 1986). It catches prey by surface plunging (Ashmole 1971) and exploits mainly the first few metres of the water column (Le Corre 1997). It feeds mainly on surface-dwelling prey, mainly flying fish and squid (Schreiber & Clapp 1987).

Red-tailed tropicbirds breed seasonally during summer in most places where they have been studied (Schreiber & Ashmole 1970, Fleet 1974, Diamond 1975, Prys-Jones & Peet 1980, Le Corre 2001). Although numerous environmental factors can reduce the number of offspring produced, it is generally accepted that food is the main ultimate factor that shapes the seasonal breeding regimes of seabirds at high latitudes (Lack 1968, Perrins 1970, Immelmann 1971, Dann et al. 1988). Tropical seabirds, on the other hand, have evolved a wide range of breeding regimes to fit with their local conditions (e.g. Harris 1969, Ashmole 1971).

Our first aim was to test the hypothesis that some changes in food availability occur seasonally and might explain the summer breeding regime of red-tailed tropicbirds at Europa island. Secondly, we assessed the hypothesis that the food availability of breeding adults might vary between years as a result of unpredictable changes in the environment. Our predictions were:

(1) If the marine environment where red-tailed tropicbirds of Europa island forage has seasonal variations, then the diet composition should vary seasonally. (2) If the marine environment shows inter-annual variations during the course of our study, then the food available to seabirds might vary among years, and thus the diet, feeding frequency, meal size and chick body-condition should vary among years. (3) Inter-annual variations of the environment might also modify the cost of foraging for chick-rearing adults, and this might lead to inter-annual variations in the condition of breeding adults. However, the importance of these inter-annual variations in adult condition will depend on the allocation strategy of the energy of adults toward reproduction or survival.

Thus, we examined seasonal and inter-annual variations in the diet and prey size of the breeding red-tailed tropicbird at Europa Island. We also examined interannual variations in feeding frequency, and chick and adult body condition during 3 consecutive chick-rearing periods.

Many studies conducted in temperate or arctic waters have shown that changes in the diet of seabirds were correlated with changes in prey abundance and marine prey stocks (e.g. Montevecchi & Myers 1995, 1996, Furness & Camphuysen 1997, Litzow et al. 2000). Few comparable data are available in tropical areas, but this correlation is likely to be the same, as tropical seabirds are opportunistic predators. Thus we assume that any important change in food availability which may have occurred during the course of our study should have led to some change in diet, feeding frequency or body condition of chicks and possibly adults.

MATERIALS AND METHODS

Study area and bird biology. Fieldwork was carried out between 1 December 1994 and 7 May 1997 at Europa Island, southern Mozambique Channel (22° 20′ S, 40° 22′ E, Fig. 1). Red-tailed tropicbirds are medium-sized colonial seabirds (740 to 900 g, authors' unpubl. data). A single egg is laid, with the possibility of re-laying until brooding if the first attempt fails. Both parents share parental care throughout the breeding cycle. The incubation lasts 42 d and chick-rearing 85 to 90 d. At Europa Island, the red-tailed tropicbird is the only seabird that breeds mainly during austral summer (Le Corre 2001). The main peak of laying occurs from mid-November to late December, and the chick-rearing
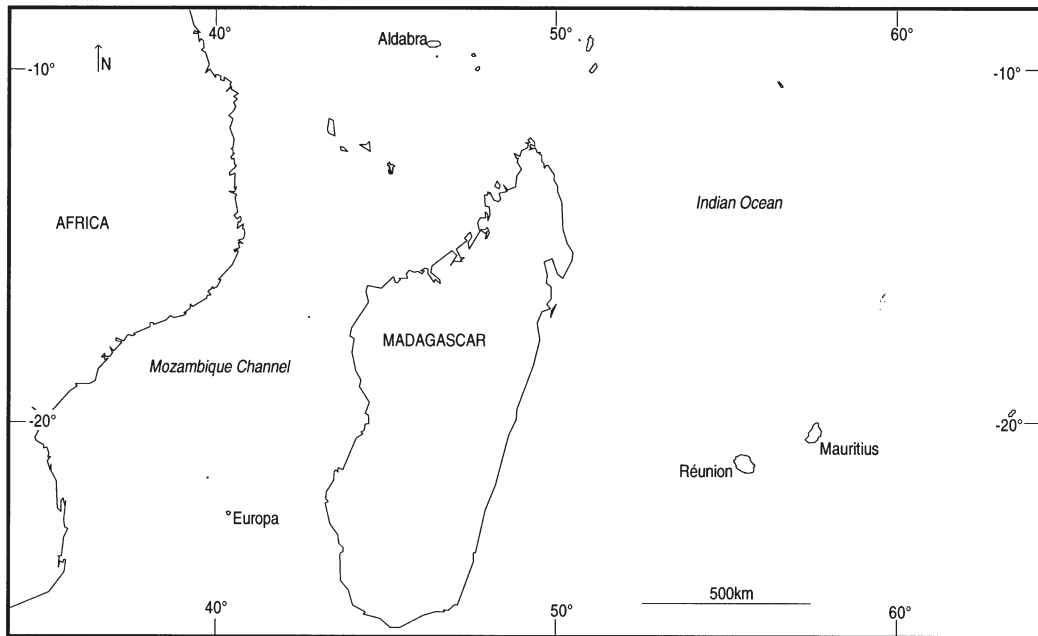
Fig. 1. Location of Europa Island in the western Indian Ocean

period occurs from February to May with most fledglings leaving the island before mid-May (Le Corre 2001). In spite of this seasonal and synchronous breeding pattern, a few birds lay until March, and rear the chick up to September each year.

Collection of food samples in the field. Adults and chicks regurgitated spontaneously when handled. We collected food samples on December 1994 and January 1995 from incubating adults as they arrived from their foraging trips to replace their mate (52 food samples), and in March to April 1995, 1996 and 1997 from chicks, just after the meal was delivered by an adult (28 in 1995, 42 in 1996 and 73 in 1997). We also obtained food samples from late breeders incubating in March and April, while most other birds were rearing chicks (10 regurgitates from incubating adults in March to April 1995 and 25 in March to April 1996). Each bird was handled only once to limit disturbance. Food samples were frozen and returned to the Centre d'Etudes Biologiques de Chizé, France, for analysis.

Food sample analysis. In the laboratory, each sample was weighed, items were then separated from each other and weighed separately. Both adults and chicks sometimes regurgitated a large number of cephalopod beaks, which had accumulated in the gizzard. Fresh prey items were washed with water and separated from accumulated ones. Identification of prey were made using Smith & Heemstra (1986) for fishes, Clarke (1986) and Nesis (1987) for squid, and our own reference collection. We measured fork length (FL, to the nearest 0.1 mm), caudal length (CL, to the nearest

0.1 mm) and fresh mass (M to the nearest 0.1 g) of all intact fish, and dorsal mantle length (ML, to the nearest 0.1 mm), lower rostral length (LRL, to the nearest 0.01 mm) and fresh mass (M) of all intact squid. We were then able to determinate allometric relationships between CL and FL, and between CL and M for the 2 main fish categories: dolphin fish (Coryphaenidae, 13 intact specimens) and flying fish (Exocoetidae, 13 intact specimens). We used the same equations for both species of dolphin fish (*Coryphaena equiselis* and *C. hippurus*), as there is no difference in body proportions of these 2 species at early stages of their life (Palko et al. 1982). Numerous partially digested flying fish were unidentifiable. Most species having similar body proportions in the area (Smith & Heemstra 1986), we determined equations for all intact specimens (most of them being *Hirundichthys* sp.), and used them for all partially digested flying fish to reconstitute fresh mass and length. We established relationships between LRL and ML, and between LRL and M of the main squid, *Sthenoteuthis oualaniensis* (Ommastrephidae, 40 intact specimens). The equations used to reconstitute the mass and length of partially digested prey were:

Sthenoteuthis oualaniensis (n = 40):

$$M\ (g)\ =\ 3.706 \times LRL^{2.247}\ (R^2 = 0.839,\ p < 0.001) \qquad (1)$$

$$ML\ (mm)\ =\ 23.442 \times LRL + 36.111$$
$$(R^2 = 0.707,\ p < 0.001) \qquad (2)$$

Coryphaena hippurus and *C. equiselis* (n = 13):

$$M\ (g)\ =\ 0.127 \times CL^{1.664}\ (R^2 = 0.796,\ p < 0.001) \qquad (3)$$

FL (mm) $= 1.915 \times CL + 103.261$ ($R^2 = 0.758$, p < 0.01) (4)

Exocetidae (mostly *Hirundichthys* sp., n = 13):

M (g) $= 0.030 \times CL^{2.061}$ ($R^2 = 0.901$, p < 0.001) (5)

FL (mm) $= 2.828 \times CL + 51.205$ ($R^2 = 0.809$, p < 0.001) (6)

For other prey species, for which the sample sizes were too small to estimate allometric equations, we used only biometrics of intact specimens for size and mass analysis.

The accumulated beaks of squid were sorted out and identified using Clarke (1986) and our own reference collection. All intact lower beaks were measured (LRL, to the nearest 0.01 mm), in order to calculate the mass and length using Eqs. (1) & (2) (*Stenoteuthis oualaniensis* only).

Foraging trip duration and feeding frequency. We measured the duration of foraging trips of incubating and chick-rearing adults. Both parents of 24 incubating pairs were colour-marked, and the identity of the adult at nest was checked once daily during 1 mo in December 1994 and January 1995. During the chick-rearing periods of March to April 1995 and 1996, both parents of 10 chicks were also colour-marked and the nests were observed continuously from sunrise to sunset during 10 d in 1995 and 15 d in 1996. When an adult arrived to feed the chick, we noted the identity of the bird and the time of arrival.

Daily mass change of the chicks. Eight to 22 chicks were studied during 11 to 15 d each year. Studied chicks were 45 to 65 d old at the beginning of the study. Chicks were weighed twice daily at sunrise (06:00 h) and sunset (18:00 h). All chicks lost mass at night thus indicating that there was no nocturnal feeding (see also Diamond 1975). The 10 pairs observed continuously to determine the duration of foraging trips and feeding frequency (see above) were included in this study of daily mass change. Thus, using the data on feeding frequency and daily mass change, we determined the relationship between the number of meals received by a chick and the daily mass change. Using this relation, we determined (for the 3 yr and for all the chicks weighed twice daily) the proportion of chicks fed at least once daily. We used the daily mass change by chicks (in grams and in %) for the 3 yr as an indicator of the chick-rearing activities of the adults.

Body condition of adults and chicks. We determined body condition of chick-rearing adults during the 3 yr. At Europa the mass of chick-rearing adults was stable throughout the chick-rearing period, except during the first 15 d, during which the mass of adults decreased (authors' unpubl. data). Thus we measured (wing chord and culmen length) and weighed 17 to 74 adults each year, chosen randomly in the colonies while rearing chicks at least 20 d old. Adults were measured and weighted just after they had fed their chick. There was a weak but significant relationship between wing chord and mass of chick-rearing adults (multiple regression analysis with the mass as a dependent variable, and wing chord and culmen length as independent variables, $R^2 = 0.07$, $F_{(2,122)} = 5.72$, p < 0.01, effect of wing chord: p = 0.002, effect of culmen length: p > 0.05). We thus calculated a body condition index (BCI) using the following equation:

$$BCI = 1 - (residual\ OM)/TM \qquad (7)$$

where OM is the observed mass (g), TM is the theoretical mass (g) calculated with the linear regression between mass and wing chord, and residual OM is the difference between TM and OM. With this equation, a BCI of 1 means that the adult has its normal mass according to its wing chord; BCI < 1 means that the bird is lighter than expected (low body condition) and a BCI > 1 means that the bird is heavier than expected (high body condition).

We also estimated the body condition of chicks during the 3 yr of study. For this purpose, we weighed and measured 44 to 74 chicks each year. At Europa, the growth of red-tailed tropicbirds lasts 85 to 90 d. Wing length was used to estimate the age of all chicks studied, using growth curves obtained at Europa (authors' unpubl. data). Wing chord increases linearly throughout growth, whereas body mass reaches an asymptotic value at the age of 60 d (wing chord > 250 mm, authors' unpubl. data). Thus, there is a significant linear relation between wing chord and mass for chicks until the age of 60 d ($R^2 = 0.33$, p < 0.01, n = 76); this relation is non-significant after that age ($R^2 = 0.02$, p > 0.05, n = 106). We calculated a BCI for each chick of less than 60 d (wing chord < 250 mm) using the same equation as for adults (see above). For chicks older than 60 d we used the mass to estimate the condition of the chicks.

Statistics. We made statistical treatments with STATISTICA for Windows (StatSoft France 2000). Values are means ± SE, significance at 0.05 level.

RESULTS

Diet composition

The average fresh mass of the 230 food samples collected during the study was 71.0 ± 3.7 g (range 1.5 to 274.4 g). Each food sample contained on average 2.7 ± 0.1 fresh prey items (range 0 to 9) and 15.6 ± 2.9 accumulated prey items, the latter being beaks of cephalopods only (range 0 to 402). Fresh prey consisted of fish and squid in similar proportions by number (respectively 49 and 51%), but fish largely outnumbered squid by mass (respectively 77 and 23%, Table 1).

Table 1. *Phaethon rubricauda*. Fresh prey items of breeding birds at Europa Island (1994 to 1997)

	Occurrence in food samples		Number		Reconstituted mass	
	N	%	N	%	g	%
Fish	**187**	**81.3**	**300**	**49.1**	**13 527.6**	**76.6**
Gonostomatidae						
Unidentified Gonostomatidae	1	0.4	1	0.2	19.8	0.1
Antennariidae						
Antennarius sp.	3	1.3	3	0.5	43.6	0.2
Unidentified Antennariidae	1	0.4	1	0.2		
Belonidae						
Ablennes hians	1	0.4	1	0.2	16.2	0.1
Tylosurus crocodilus	15	6.5	17	2.8	589.7	3.3
Unidentified Belonidae	12	5.2	12	2.0	312.7	1.8
Hemiramphidae						
Oxyporamphus micropterus	8	3.5	8	1.3	115.9	0.7
Unidentified Hemiramphidae	12	5.2	13	2.1	103.4	0.6
Exocoetidae						
Cheilopogon furcatus	1	0.4	1	0.2	65.8	0.4
Cypselurus sp.	2	0.9	3	0.5	136.0	0.8
Exocoetus sp.	4	1.7	4	0.7	254.3	1.4
Hirundichthys speculiger	4	1.7	4	0.7	106.9	0.6
Hirundichthys sp.	3	1.3	4	0.7	210.6	1.2
Paraexocoetus brachypterus	1	0.4	1	0.2	36.9	0.2
Unidentified Exocoetidae	53	23.0	69	11.3	3703.1	21.0
Mullidae						
Unidentified Mullidae	1	0.4	1	0.2	26.8	0.2
Bramidae						
Unidentified Bramidae	1	0.4	1	0.2	20.1	0.1
Carangidae						
Caranx hedlandensis	1	0.4	1	0.2	36.9	0.2
Decapterus sp.	2	0.9	2	0.3	158.0	0.9
Naucrates ductor	1	0.4	1	0.2	21.8	0.1
Selar sp.	2	0.9	4	0.7	19.1	0.1
Unidentified Carangidae	7	3.0	8	1.3	42.7	0.2
Coryphaenidae						
Coryphaena equiselis	23	10.0	31	5.1	2415.2	13.7
Coryphaena hippurus	21	9.1	22	3.6	2490.9	14.1
Coryphaena sp.	20	8.7	22	3.6	1401.2	7.9
Scaridae						
Unidentified Scaridae	1	0.4	1	0.2	20.0	0.1
Scombridae						
Auxis rochei	1	0.4	1	0.2	56.3	0.3
Sarda sp.	1	0.4	1	0.2	48.1	0.3
Unidentified Scombridae	13	5.7	15	2.5	581.6	3.3
Tetraodontidae						
Lagocephalus lagocephalus	5	2.2	5	0.8	170.7	1.0
Diodontidae						
Unidentified Diodontidae	1	0.4	1	0.2	5.0	0.0
Unidentified fish	36	15.7	41	6.7	298.3	1.7
Cephalopods	**139**	**60.4**	**311**	**50.9**	**4126.5**	**23.4**
Ommastrephidae						
Sthenoteuthis oualaniensis	74	32.2	140	22.9	2723.2	15.4
Ornithoteuthis volatilis	1	0.4	1	0.2	11.7	0.1
Unidentified Ommastrephidae	60	26.1	114	18.7	1220.4	6.9
Onychoteuthidae						
Unidentified Onychoteuthidae	6	2.6	6	1.0	81.2	0.5
Unidentified squids	45	19.6	49	8.0	82.9	0.5
Tremoctopodidae						
Tremoctopus violaceus	1	0.4	1	0.2	7.1	0.0
Total			**611**	**100.0**	**17 654.1**	**100.0**

Fresh prey items

A total of 611 fresh prey items were found in the food samples. Most prey were identified to family level (86% of the fish and 84% of the cephalopods, Table 1). Three families, namely the squid Ommastrephidae, the fishes Exocoetidae (flying fish) and Coryphaenidae (dolphin fish) accounted for 68% of the fresh prey by number and 83% by mass, though all prey were represented by 13 fish families and 3 cephalopod families (Table 1). Among Ommastrephidae, all identified items (n = 140) but one belonged to a single species, *Sthenoteuthis oualaniensis*, strongly suggesting that most Ommastrephids caught by red-tailed tropicbirds were *S. oualaniensis*. We identified 6 different taxa of flying fish, most of them being *Hirundichthys speculiger* and *Hirundichthys* sp. The 2 species of dolphin fish (*Coryphaena equiselis* and *C. hippurus*) were recovered in similar proportions. Among other prey families, Belonidae (needle fish, mostly *Tylosaurus crocodilus*), Hemiramphidae (half-beaks), Scombridae (tunas and allies) and Carangidae (carangids) ranked 4, 5, 6 and 7 respectively and accounted for 14.0% of the fresh prey items by number (11.9% by mass). Other taxa (7 fish families and 2 cephalopod families) were rare, occurring less than 10 times in the food samples (Table 1).

Accumulated cephalopod beaks

Large numbers (>20 per regurgitate) of accumulated beaks were present in 17.7% of the food samples, totalling 2448 lower beaks. We determined 8 different taxa of cephalopods, belonging to 4 families of squid (order Teuthida) and 2 families of pelagic octopuses (order Octopoda, Table 2). The most abundant squid was *Sthenoteuthis oualaniensis* (90% of the beaks, Table 2) following by the pelagic octopus *Tremoctopus violaceus*. The 8 other taxa were very rare, indicating that they were exceptionally caught by red-tailed tropicbirds at Europa Island.

Prey size

Using direct measurements and Eqs. (1) to (6), we obtained the mass or length of 44.9% of the fresh prey items (Table 3). The size and mass of the prey varied greatly from 36 to 370 mm (mean = 126 ± 63 mm, n = 261) and from 2.8 to 197.0 g (mean = 49.4 ± 44.3 g, n = 241, Table 3). Squid were smaller and lighter than fish, and dolphin fish were twice as heavy than the average other fish prey (dolphin fish: 120.0 g; other fish: 63.4 g).

Seasonal dietary changes

Food samples contained more prey (3.2 ± 0.2) during chick-rearing than during incubation (1.8 ± 0.1, 1-way ANOVA: $F_{1, 228}$ = 39.8, p < 0.001), and they were heavier during chick-rearing (96.6 ± 4.3 g) than during incubation (27.2 ± 2.7 g, 1-way ANOVA: $F_{1, 228}$ = 133.4, p < 0.001). There was considerable seasonal variation in diet composition (Fig. 2A). During incubation the commonest prey were squid (mostly *Sthenoteuthis oualaniensis*) and flying fish. When considering diet composition by mass, flying fish were the dominant species, squid ranked second and the other fish represented less than 20% of the diet. During chick-rearing (1995 to 1997 pooled together, see below), the commonest prey were first squid (*S. oualaniensis*), second dolphin fish and third flying fish. When considering

Table 2. *Phaeton rubricauda*. Cephalopods identified from accumulated prey items of breeding birds at Europa Island (1994 to 1997). 'Number' column is for lower beaks only. Family ranked from most abundant to least abundant prey species

	N	Frequency (%)	Family rank
Teuthida	**2331**	**95.2**	
Thysanoteuthidae	10	0.4	4
Thysanoteuthis rhombus	10	0.4	
Ommastrephidae	2234	91.3	1
Sthenoteuthis oualaniensis	2212	90.4	
Ornithoteuthis volatilis	22	0.9	
Onychoteuthidae	82	3.3	3
Unidentified Onychoteuthidae	82	3.3	
Chiroteuthidae	2	0.1	6
Chiroteuthis sp.	2	0.1	
Unidentified squids	3	–	
Octopoda	**117**	**4.8**	
Argonautidae	4	0.2	5
Argonauta argo	4	0.2	
Tremoctopodidae	112	4.6	2
Tremoctopus violaceus	112	4.6	
Unidentified octopod	1	–	
Total	**2448**	**100.0**	

Table 3. *Phaeton rubricauda*. Biometrics of fresh prey items. Tests are 1-way ANOVA and post-hoc HSD Tukey test. Values with different letters are significantly different from each other. Mean ± SE are shown

	Weight (g)	Length (mm)
Dolphin-fish	120.0 ± 5.5 (39)[a]	222.6 ± 4.5 (36)[a]
Flying-fish	70.8 ± 5.1 (49)[b]	173.5 ± 4.7 (43)[b]
Other fish Families	44.3 ± 5.7 (19)[c]	217.1 ± 1.1 (15)[a]
Squids	20.6 ± 1.1 (134)[d]	84.3 ± 1.1 (167)[c]
Test	p < 0.001	p < 0.001

A : Seasonal variations

■ Squid
□ Flying fish
⊠ Dolphin fish
⊞ Needle fish
☰ Scombrids
▨ Other fish families

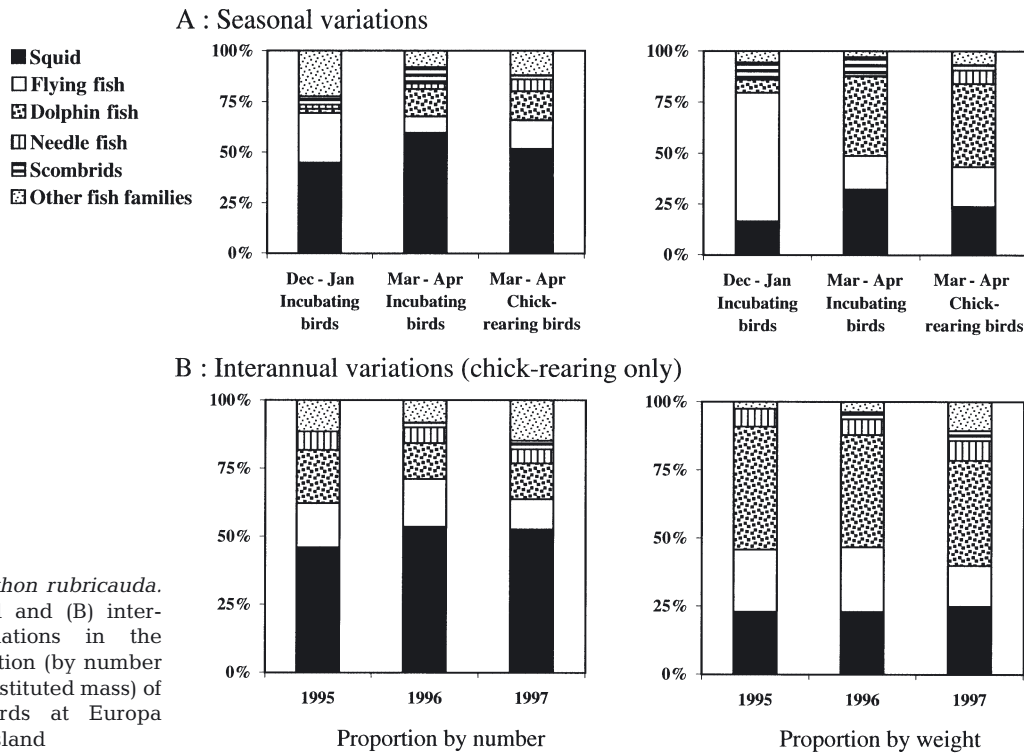## B : Interannual variations (chick-rearing only)

Fig. 2. *Phaethon rubricauda.* (A) Seasonal and (B) inter-annual variations in the diet composition (by number and by reconstituted mass) of breeding birds at Europa Island

Proportion by number

Proportion by weight

the importance of prey by mass, dolphin fish ranked first (41%), squid second (24%) and flying fish third (20%). These seasonal variations were significant when considering proportions by number (χ^2 = 28.29, df = 5, p < 0.001) and by mass (χ^2 = 68.79, df = 5, p < 0.001).

There were no differences in the diet of birds incubating in March to April of 1995 and 1996 (χ^2 = 0.66, df = 3, p > 0.05). Thus, we pooled the data to compare the diet of birds in March to April, in relation to their breeding stage. In March to April, breeding birds had a comparable diet composition whatever the breeding stage (χ^2 = 6.45, df = 5, p > 0.05, Fig. 2A). By contrast, the diet of birds incubating in December to January was very different (χ^2 = 16.09, df = 5, p < 0.01, Fig. 2A).

The squid *Sthenoteuthis oualaniensis* caught in December to January were smaller than those caught in March to April (Table 4). Birds incubating in March to April caught squid of the same size as adults rearing a chick in the same period (Table 4), suggesting that the observed increase of squid size from December to April was not due to different prey selection of birds in relation with their breeding stage.

Inter-annual dietary changes during the chick-rearing period

There was no inter-annual variation in the mean mass of food samples collected from chicks (1-way

ANOVA, $F_{2,142}$ = 0.47, p > 0.05, Table 5), nor in the diet composition (Fig. 2B). This was true when considering the importance of each prey category by number (χ^2 = 12.21, df = 10, p > 0.05) and by mass (χ^2 = 13.06, df = 10, p > 0.05). There were no inter-annual differences in the size or mass of the 2 main prey, namely the squid *Sthenoteuthis oualaniensis* and dolphin fish (Table 4).

Duration of foraging trips and feeding frequency

Foraging trips lasted 1 to 9 d (mean 4 ± 2 d) during incubation and 6 to 78 h (mean 34 ± 14 h or 1.4 ± 0.6 d) during the chick-rearing period (Fig. 3). During chick-rearing, all feedings occurred during daytime, mostly between 08:00 and 13:00 h (Fig. 4). Foraging trips of chick-rearing adults were shorter in 1995 and longer in 1996 (Table 5). Consequently, the number of meals received daily per chick was higher in 1995 than in 1996.

Daily mass change of the chicks and proportion of chicks fed daily

Chick daily mass change was proportional to the number of meals received daily (R^2 = 0.64, p < 0.01, Table 6). Most chicks that received at least 1 meal per day had a positive daily mass change (91 and 100% of

the chicks that had received 1 and 2 meals per day, respectively). Thus we considered that chicks that had lost mass during a day received no meal during that day. This may lead to a slight underestimation of the proportion of chicks fed per day, as 9% of the chicks which received 1 meal during a day lost between 5 and 20 g. However, we considered that this cause of underestimation was constant for the 3 yr, and did not prevent us from investigating inter-annual variation in proportion of chicks fed per day. On average, 79% of the chicks were fed at least once a day, but there were significant inter-annual variations: chicks were fed less often in 1996 when compared to 1995 and 1997 (Table 5), which is consistent with the fact that the observed feeding frequency was lower in 1996 (see above). The daily mass change averaged 69 g but, again, there was inter-annual variation: chicks received less food daily in 1996 compared to 1995 and 1997 (Table 5).

We investigated, for each study period, day-to-day variations in daily mass changes. We found significant day-to-day variations in the daily mass change in 1996 (1-way ANOVA: $F_{13.224} = 3.53$, $p < 0.01$) but not in 1995 ($F_{9.85} = 0.62$, $p > 0.05$) nor 1997 ($F_{14.105} = 1.34$, $p > 0.05$).

Adult and chick body condition

There was no inter-annual variation either in body condition or in mass of chick-rearing adults (Table 7). Chicks at fledging were 15% heavier than adults, and their condition was stable throughout the study (Table 7). However, chicks of less than 60 d tended to have a poorer condition in 1997 compared to 1995, with 1996 being an intermediate year (Table 7).

DISCUSSION

Feeding ecology

Diet composition

A regional comparison of the diet of red-tailed tropicbirds is given in Table 8. As with most tropical

Table 4. *Phaethon rubricauda*. Seasonal and inter-annual variation in size and mass of the 2 main prey items at Europa Island: (a) squid *Sthenoteuthis oualaniensis*, accumulated and fresh items pooled; and (b) the fish *Coryphanea* spp., fresh items. Dorsal mantle lengths (DML) was measured for *S. oualaniensis* and total length (TL) for *Coryphaena* spp. (mean ± SE are shown). One-way ANOVA and post-hoc HSD Tukey test were used to analyse data. NS: non-significant

	N	Length (mm)	Mass (g)
(a) *Sthenoteuthis oualaniensis*			
Incubation			
December 1994 to January 1995	145	79.3 ± 0.9[a]	15.9 ± 0.7[a]
March to April 1995	85	82.2 ± 1.7[a,b]	19.6 ± 1.6[a,b]
March to April 1996	65	85.9 ± 1.2[b]	21.1 ± 1.0[b]
Chick-rearing (March to April)			
1995	246	84.5 ± 0.8[b]	20.6 ± 0.8[b]
1996	522	84.9 ± 0.6[b]	21.3 ± 0.7[b]
1997	844	83.8 ± 0.5[b]	20.1 ± 0.4[b]
Test		p < 0.01	p < 0.01
(b) *Coryphaena* spp.			
Chick-rearing (March to April)			
1995	8	222.9 ± 4.8	124.4 ± 8.2
1996	14	229.9 ± 9.9	130.3 ± 11.4
1997	15	218.3 ± 5.4	113.3 ± 7.6
Test		NS	NS

Table 5. *Phaethon rubricauda*. Mass of food samples, daily mass changes of chicks and chicks' feeding frequency (mean ± SE). Values with different letters are significantly different from each other. *p < 0.05, ***p < 0.001. NS: non-significant

| Study period	No. of chicks (beginning; end)	N (d × chick)	Chick mass (g) Beginning	End	Mean mass of food samples	Daily mass change (g) g	%	Foraging trip duration (h)	Feeding frequency (meals d⁻¹)	Proportion of chicks fed daily
28 March to 7 April 1995	11; 9	95	858±32[a]	896±34	96.4±58.3 (30)	84.2±7.6[a]	9.6±0.9[a]	32.4±1.5	1.27±0.10	84/95 (88.4%)
27 March to 9 April 1996	22; 16	238	824±19[a,b]	815±24	102.9±52.1 (42)	52.4±5.7[b]	6.7±0.7[b]	38.4±1.6	0.98±0.05	168/238 (70.6%)
23 March to 6 April 1997	8; 8	120	763±31[b]	881±24	93.1±49.3 (73)	92.4±6.8[a]	11.1±0.8[a]	–	–	108/120 (90.0%)
Total	41; 33		821±15	853±17	96.6±51.9 (145)	69.7±3.9	8.5±0.5			360/453 (79.4%)
Tests			*[1,2]	NS[1]	NS[1]	***[1,2]	***[1,2]	*	*	***[3]

[1]One-way ANOVA; [2]Post-hoc HSD Tukey test; [3]χ^2 test
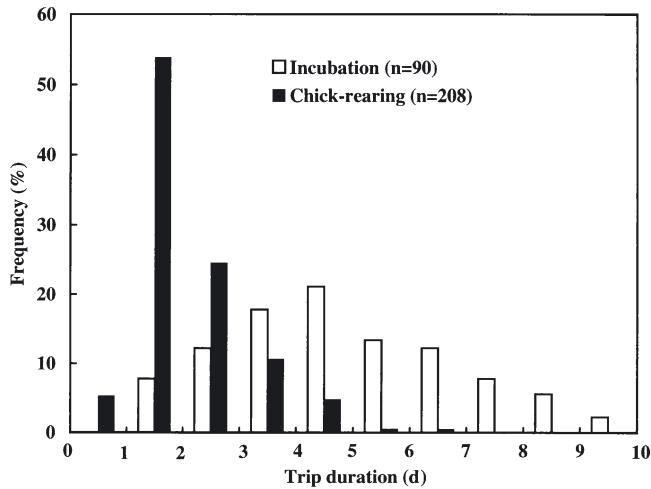
Fig. 3. *Phaethon rubricauda.* Duration of foraging trips in relation to the breeding stage of adults at Europa Island

Fig. 4. *Phaethon rubricauda.* Distribution of feedings to chicks throughout the day in 1995 and 1996

seabirds, red-tailed tropicbirds feed on surface-dwelling squid and fish throughout their range. Fish being generally heavier than squid, the proportion by mass (or volume) is always higher for fish than for squid. At Europa, both prey categories were in equal proportions by number, but fish always exceeded squid by mass.

The main difference in the diet of red-tailed tropicbirds at Europa Island, when compared with previous studies, was the importance of dolphin fish. They ranked third when considering the whole breeding
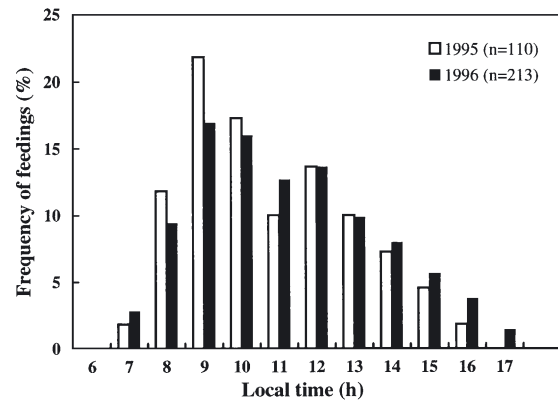
season, after the squid *Sthenoteuthis oualaniensis* and flying fish, but ranked first by mass (41%) during the 3 chick-rearing seasons. Dolphin fish never represented more than 10% of the mass of food at all other places studied, including the nearby Aldabra Island. This abundance suggests that dolphin fish were more abundant around Europa Island in March to April than at other studied areas. Red-tailed tropicbirds are known to catch very large prey by comparison with other medium-sized seabirds (Ashmole & Ashmole 1967, Harrison et al. 1983). At Europa, chick-rearing adults frequently carried prey of 120 g (mean mass of a dolphin-fish), equivalent to 16% of their body mass (up to 197 g, or 26% of the adult mass for the heaviest dolphin fish found in a food sample). Strong bill, large gape and powerful flight probably allow such performances.

Implications of the diet composition for foraging birds

Oceanic tropical seabirds exploit large marine areas in which prey have a sparse, patchy and unpredictable

Table 6. *Phaethon rubricauda.* Relation between number of meals received per day and daily mass change of chicks (mean ± SE and range)

	0 meal	1 meal	2 meals	3 meals
N	53	113	55	2
Mass change (g)	−37.4 ± 2.3	67.9 ± 4.4	135.5 ± 8.2	235.0 ± 25.0
Range (g)	−80 to 0	−20 to +200	5 to 320	210 to 260
Mass change (%)	−4.5 ± 0.3	8.6 ± 0.6	16.2 ± 1.0	27.3 ± 2.8
Range (%)	−8.9 to 0.0	−3.7 to +33.3	0.5 to 35.7	24.6 to 30.1

Table 7. *Phaethon rubricauda.* Body condition and mass of chick-rearing adults and chicks at Europa Island during 3 breeding seasons. Values with different letters are significantly different from each other. *p < 0.05, NS: non-significant

Year	Chick-rearing adults			Chick (wing < 250 mm)			Chick (wing > 250 mm)	
	N	Body condition	Mass (g)	N	Body condition	Mass (g)	N	Mass (g)
1995	17	1.01 ± 0.01	757 ± 10	18	1.08 ± 0.03[a]	860 ± 32[a]	26	890 ± 13
1996	74	1.00 ± 0.01	749 ± 5	22	1.01 ± 0.02[a,b]	769 ± 25[a,b]	42	859 ± 17
1997	45	0.99 ± 0.01	737 ± 7	36	0.96 ± 0.02[b]	741 ± 19[b]	38	853 ± 12
Test		NS[1]	NS[1]		*[1,2]	*[1,2]		NS[1]
[1]One-way ANOVA; [2]post-hoc HSD Tukey test								

Table 8. *Phaethon rubricauda*. Comparison of the diet at different breeding localities

Locality (latitude)	No. of food samples	% fish and squid By number		% fish and squid By mass		Main prey item Fish	Main prey item Squid	Average length of the prey (mm) Fish	Average length of the prey (mm) Squid	Variation Seasonal	Variation Inter- annual	Source
		Fish	Squid	Fish	Squid							
Hawaii (27°N)	270	63	37	82	18	Flying fish, carangids	*Sthenoteuthis oualaniensis*	130–160	80–90	Yes	–	Harrison et al. (1983)
Christmas, Pacific Ocean (3°N)	49	33	67	53	47	Flying fish	*Sthenoteuthis oualaniensis*	100–120	60–80	–	–	Ashmole & Ashmole (1967)
Aldabra (9°S)	62	57	43	73	27	Flying fish	Ommastrephidae	120–180	60–100	No	–	Diamond (1975)
Christmas, Indian Ocean (10°S)	28	50	50	–	–	Flying fish	Unspecified	–	–	–	–	Gibson-Hill (1947)
Europa (21°S)	230	49	51	73	27	Flying fish, dolphin fish	*Sthenoteuthis oualaniensis*	150–250	70–90	Yes	No	This study

distribution (Lack 1968, Ashmole 1971). In the white-tailed tropicbird (*Phaethon lepturus*), and supposedly in most pelagic seabirds, chick-rearing adults forage in the open sea and strive to collect a 'target payload mass' as quickly as possible (Schaffner 1990). In this context, dolphin fish are of considerable interest, as a single prey may correspond to this target payload mass. Thus chick-rearing red-tailed tropicbirds probably search for dolphin fish actively. However, these prey are less abundant than squid, as they represent 'only' 15% of the prey by number during the chick-rearing period (51% for squid). Thus, at Europa the diet of chick-rearing adults is composed of less common but very profitable prey (dolphin fish), and of more common but less profitable prey (squid and small fish). Dolphin fish concentrate near the surface under drifting objects (e.g. Deudero et al. 1999). Foraging red-tailed tropicbirds might search those drifting objects to increase their chance of catching a dolphin-fish. Indeed, at sea observations have shown that in the western Indian Ocean, tropicbirds are attracted by drifting objects (including ships), whereas other sea-birds are not (M. Le Corre & S. Jaquemet unpubl. data).

Foraging range

The foraging range of breeding red-tailed tropicbirds is not known, as no tracking has been conducted yet. At Europa, foraging trips lasted on average 4 d during incubation, and 34 h during chick-rearing. Assuming firstly that foraging adults spent at least 8% of the duration of the trip flying in a straight line from the nest (figure based on radio tracking of chick-rearing white-tailed tropicbirds, Pennycuick et al. 1990), and secondly that the mean flight-speed of birds commuting from their nest to foraging areas is 50 km h^{-1} (Spear & Ainley 1997), one can estimate a theoretical

foraging radius. This calculation gives a value of 384 km during incubation and of 136 km during the chick-rearing period. This suggests that red-tailed tropicbirds can forage far from their breeding places, as already suspected by previous authors (Diamond 1975, Schreiber & Clapp 1987).

Seasonal variations in diet

Our results on diet composition show that there are seasonal variations in diet. Birds incubating in March to April (late breeders) had the same diet as birds rearing chicks in the same period ('normal' breeders), suggesting that seasonal variations in diet were due to true changes in prey availability and not to changes in prey selection according to the breeding stage. The main seasonal variation in diet was the appearance of dolphin fish during March to April, which, for most birds, corresponds to the chick-rearing period. Dolphin fish are fast-swimming fish widely distributed in the warm tropical waters (review in Palko et al. 1982). They migrate in relation to seasonal changes in sea-surface temperature and are more abundant during summer at the poleward limits of their range (Palko et al. 1982). Sea-surface temperatures in the Mozambique Channel are elevated all year round but show sharp seasonal variations, especially in the south, where the cool subtropical waters shift northward during winter (Piton 1993, Donguy & Meyers 1996, Villacastin-Herrero et al. 1996). Surface waters around Europa Island are warmest in January, February and March (27 to 28°C) and coldest in July, August and September (23 to 24°C, Piton et al. 1981, Le Corre 2001). This may explain why both *Coryphaena hippurus* and *C. equiselis* occurred seasonally in the diet of chick-rearing red-tailed tropicbirds. Note that *C. equiselis* had never been formally identified in the Mozam-

bique Channel, nor in South African waters (Palko et al. 1982, Smith & Heemstra 1986).

The second seasonal variation in diet was the change in length and mass of the squid *Stenoteuthis oualaniensis.* These squid were larger during March to April than during December to January. This squid occurs in 3 different forms in the Indian Ocean, distinguished by mature females, but only the widespread middle-sized form occurs in the southern Mozambique Channel (Nesis 1993). The increasing size of squid caught by red-tailed tropicbirds between November and April may be due to the growth of squid born during early summer.

We studied a complete breeding cycle during 1 yr only (from November 1994 to April 1995), and thus cannot ascertain that the seasonal pattern found during that breeding cycle occurred annually. However, the fact that the diet of red-tailed tropicbirds was the same during 3 consecutive chick-rearing periods (see below) suggests that the pattern observed during the 1994/95 cycle may have also occurred in 1995/96 and 1996/97.

The red-tailed tropicbird is not the only seasonal breeder of the seabird community of Europa, but it is the only species that breeds mainly in summer (Le Corre 2001). Other seasonal breeders (Audubon's shearwater *Puffinus lherminieri*, red-footed boobies *Sula sula* and sooty tern *Sterna fuscata*) breed during the austral winter and all of them are gregarious species associated with surface-dwelling tunas. It has been argued that the winter breeding regimes of these species may be due to an increase in tuna abundance during winter, in relation with the northward shift of cool waters during winter (Le Corre 2001). The summer breeding regime of red-tailed tropicbird, on the other hand, may have been advantaged by seasonal variations of the abundance of dolphin fish in the southern Mozambique Channel. Further studies on seasonal movements of dolphin fish in this area would be of great interest in addressing this question.

Inter-annual variations

Diet composition

During the chick-rearing period, 64% of the food brought to the chicks included only 3 prey species, namely the 2 closely related dolphin fish (41%) and the squid *Stenoteuthis oualaniensis* (23%). Accordingly, any inter-annual variations in the abundance of these key-species should have strong effects on the growth, body condition and survival of chicks, and possibly on the body condition of adults. We did not find any inter-annual variations in the frequency and size of these

prey during our 3 yr study, suggesting that no major change in their abundance have occurred during our study. These results will be discussed below, together with those obtained on feeding rate, and on chick and adult body condition.

Feeding frequency, daily mass change and chick body condition

Chick-rearing adults made longer foraging trips in 1996 compared to 1995, which resulted in a reduced feeding frequency in 1996. This could have been due to a greater difficulty of adults to find prey in 1996. Indeed the total amount of food delivered to chicks daily (estimated by daily mass change of chicks) and the proportion of chicks fed at least once a day were lower in 1996 than in 1995 and 1997. We also found intra-annual day-to-day variations in food provisioning in 1996, but not in 1995 and 1997, suggesting that food availability was less regular and predictable in 1996. Chicks of less than 60 d were in good condition in 1995 and in poorer condition in 1997, with 1996 being intermediate. However, the mass of older chicks (>60 d) did not differ among years. These results suggest that day-to-day variations in food availability may have day-to-day effects on food provisioning and body condition of chicks, but these short-term effects do not necessarily lead to inter-annual variations in the body condition of chicks at fledging. Similarly, Shea & Ricklefs (1996) found daily variations but no inter-annual variations in the growth rate of chicks belonging to 6 species of tropical seabirds at Midway Atoll (including the red-tailed tropicbird).

Adult body condition

We did not find inter-annual variation in adult body condition during the chick-rearing period. This is consistent with our findings on diet and chick condition at fledging: during our 3 yr study, the food availability has probably remained stable at the scale of the whole chick-rearing period, although short-term variations occurred.

Is the Mozambique Channel a predictable marine environment?

Our results show that during chick-rearing, the diet, feeding frequency and body condition of both fledglings and adults were essentially the same during 3 consecutive yr, suggesting that the abundance of the main prey types (dolphin fish and squids) was rela-

tively stable during this period. This contrasts with the generally accepted idea that tropical seabirds feed on unpredictable food resources. However, a 3 yr study is too short to assess the predictability and the stability of an ecosystem. Non-annual events like ENSO might reduce the abundance of prey in the Mozambique Channel. Our study was conducted from 1995 to 1997, e.g. between the ENSO events of 1994 and 1998. Only 1 study investigated the effects of ENSO events on seabirds in the tropical Indian Ocean. Ramos et al. (2002) have shown that breeding roseate terns *Sterna dougalli* of Aride Island (Seychelles) were fewer and laid later during ENSO events. Studies conducted in the Pacific Ocean have produced contradictory results. On Christmas Island and Johnston Atoll, Schreiber (1994) found that during ENSO events, chicks of red-tailed tropicbirds received less food per day and had a slower growth rate, whereas Shea & Ricklefs (1996) did not find any effects of the 1982/83 ENSO event on chick growth of 6 species of seabirds (including red-tailed tropicbirds) at Midway Atoll. Further long-term studies on the diet and body condition of tropical seabirds of the western Indian Ocean and on the biology of their prey would be of interest to estimate the impact of such unpredictable events on oceanic seabirds.

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