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The Condor 101:179–185

SYNCHRONOUS UNDERWATER FORAGING BEHAVIOR IN PENGUINS[1]

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Abstract. We used electronic time-depth recorders to examine the synchronous foraging behavior of penguins both at the surface and underwater. During a daily foraging trip in the chick guarding stage, two females of the Northern Rockhopper Penguin *Eudyptes chrysocome moseleyi* dove in synchrony over seven consecutive hours during which they performed together 286 dives between 3 and 60 m, and fed on the same prey, the swarming euphausiid *Thysanoessa gregaria.* Most of the synchronous dives began (71%) and ended (59%) with a time interval of ≤ 4 sec between birds. Differences in the duration and maximum depth of dives were slight: ≤ 2 sec for 44% and ≤ 1 m for 62% of the dives. Indirect evidence suggests that the two birds were part of a larger flock of foraging pen-

[1] Received 20 April 1998. Accepted 15 September 1998.
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guins. One bird initiated and ended 70% of the dives first and consistently dove deeper (95% of the dives) during the deep dives. The close similarity of the two time-depth profiles indicates that the penguins were visually in contact during the dives and suggests a coordinated underwater behavior to search and catch prey.

Key words: communal feeding, Eudyptes chrysocome, *food patchiness, Rockhopper Penguins, synchronous diving.*

Foraging in flocks is common in birds, including seabirds (Morse 1985, Götmark et al. 1986). In some cases, flock feeding consists of truly cooperative fishing. One of the best described of these comes from pelicans swimming together at the surface to drive fish towards shallow waters where they are more easily caught (Elliott 1992). Collaborative predation has been recorded also from seabirds diving from the air (Nelson 1978) or from the surface (Wilson and Wilson 1990, Orta 1992). In penguins and cormorants, the movements of individuals within a flock tend to be closely synchronized, with birds swimming and moving in and out of the water in unison and feeding communally (Siegfried et al. 1975, Marchant and Higgins 1990). A main limitation of these studies is that they have been restricted to visual observations of flocks at the surface, with little information on the underwater behavior of the birds. Recent advances in technology allow data collection of foraging behavior at a temporal resolution of seconds for consecutive days at sea (Wilson 1995). However, to our knowledge, no information has been gathered on the social behavior at sea of diving birds, including penguins, using such electronic devices because such studies have been conducted on a small number of birds living in very large colonies, which considerably lowers the probability that at least two equipped birds forage together.

We report here that Northern Rockhopper Penguins (*Eudyptes chrysocome moseleyi*) carrying time-depth recorders show synchronous behavior both at the surface and underwater while foraging at sea. Different parameters of each of the synchronous dives were analyzed in detail for two penguins, as was the role of each individual bird in initiating and terminating the dives. Such data give new insight into previously unrecorded underwater social behavior of seabirds.

METHODS

BIRDS AND STUDY SITE

The study was undertaken during October 1995 at a breeding colony of Rockhopper Penguins (about 200 pairs) located at Pointe d'Entrecasteaux, Amsterdam Island (37°50'S, 77°31'E), southern Indian Ocean. At that time, female Rockhopper Penguins performed daily foraging trips to feed their offspring, while males fasted ashore to guard the chicks. Females were captured in late afternoon, after their daily foraging trip, while they were near their chicks. They were released at their nest 15–20 min following capture. This timing allowed females to recover from the stress of capture and manipulation during the night before returning at sea to feed.

The diving behavior of 14 females was investigated over 1 to 3 consecutive days during the end of the chick guarding stage. Birds A and B (see below) were simultaneously studied on 25 and 26 October, over two consecutive daily foraging trips. These two females weighed 2.6 kg and 2.4 kg, and they were rearing a single chick with body masses of 0.71 kg and 1.04 kg, respectively.

TIME-DEPTH RECORDERS

Penguins were fitted with electronic time-depth recorders (TDRs; Mark V, Wildlife Computers, Woodinville, Washington). The units were 9.5 cm long × 3.7 cm wide × 1.5 cm high and weighed about 70 g, corresponding to less than 3% of the bird's body mass. TDRs were shaped to reduce drag following the suggestions of Bannasch et al. (1994). They were attached to the most caudal region of the back using quick setting epoxy and plastic tie-wraps (Kooyman et al. 1992). TDRs had a maximum storage capacity of 128 kilobytes and sampled depth every 2 sec. This recording interval is less than 10% of the mean dive duration, thus introducing no errors in dive number and dive parameters (Wilson et al. 1995). Depth resolution was ± 1 m and the time base (quartz-controlled) was the same for all the recorders.

DIVING ACTIVITY ANALYSIS

Dive records were downloaded to a PC-compatible computer into two formats: hexadecimal format for further analysis with software from Wildlife Computers, and a decimal (ASCII) format for direct investigation of depth data. A dive was deemed to occur when the depth was greater or equal to 3 m (Chappell et al. 1993).

The high level of similarity of the foraging trips performed by two birds on the same day (penguins A and B on 26 October 1995) led us to examine in detail their swimming and diving behavior to investigate the degree of synchronization. Dive parameters used in the analysis were the maximum depth, total duration, and time spent at the bottom of the dive (the amount of time spent between 75 and 100% of the maximum depth reached) for each dive. In addition, the sample rate of every 2 sec allowed us to calculate the intermediate depths reached by the penguins each second as the mean between two 2-sec consecutive records. Assuming that bird movement was linear between two consecutive records, we performed a second-by-second analysis of depths during the two foraging trips.

DIET ANALYSIS

Stomach contents of both penguins A and B were obtained using the "water off-loading technique" (Gales 1987) when they returned ashore after foraging in the afternoon of 26 October. Birds were repeatedly flushed until the returning water was clear, indicating that the stomach was empty. Dietary analysis followed Tremblay et al. (1997).

DATA ANALYSIS

Differences in dive parameters between birds A and B were analyzed with two-tailed independent *t*-tests. Differences were considered statistically significant at the 0.05 level. Means are given ± SD.

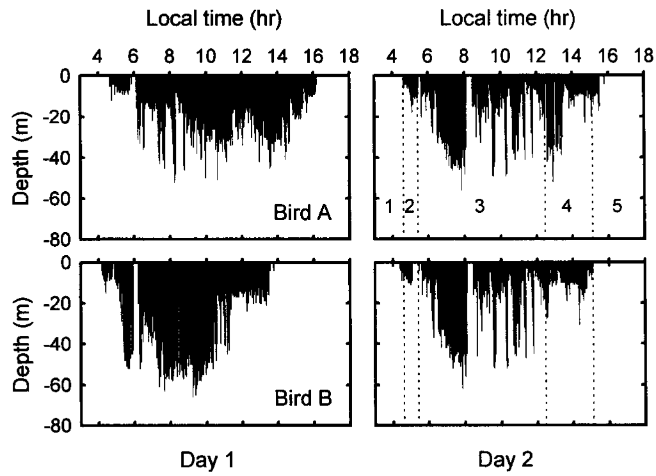

FIGURE 1. Diving records of two consecutive days for two female Northern Rockhopper Penguins at Amsterdam Island. For phases 1 to 5 see text.

RESULTS

GENERAL CHARACTERISTICS OF FORAGING TRIPS

A total of 29 foraging trips was recorded from the 14 female Rockhopper Penguins equipped with data loggers. Twenty-five of the time-depth profiles were obtained while three to five equipped birds were simultaneously at sea. Within these 25 records, only 2 (8%) showed synchronous diving behavior. Five equipped penguins were at sea on 26 October 1995: four of them performed daily foraging trips and the fifth individual was involved in a longer trip including one night. Two birds (A and B) dove in synchrony (Fig. 1), while the three other penguins had different diving profiles indicating no synchronous behavior (data not shown).

Diving patterns of birds A and B differed markedly on the first day we recorded their behavior at sea (Fig. 1). Diving profiles during the second daily foraging trip however exhibited a high level of similarity over several consecutive hours. On that day, the two female Rockhopper Penguins left the colony at dawn and returned ashore in the afternoon. The first and last diving records of birds A and B took place at 04:38 and 04:24, and at 15:49 and 15:07, respectively. Total time spent at sea was, therefore, 11 hr 11 min and 10 hr 43 min for females A and B, respectively. During these foraging trips, bird A performed 550 dives $\geq$ 3 m, and bird B 526 dives. The mean maximum diving depth and dive duration of the two penguins were not significantly different (13.4 ± 11.8 vs. 13.2 ± 12.5 m, t_{1074} = 0.27, P = 0.78, and 48.6 ± 33.9 vs. 47.5 ± 33.5 sec, t_{1074} = 0.54, P = 0.58, for birds A and B, respectively).

The two time-depth profiles were divided into 5 periods in chronological order (Fig. 1). Only one of the two penguins was at sea during periods 1 and 5 and therefore were excluded from further analysis. Periods 2 and 4 were marked by no synchronization in diving behavior, whereas period 3 was characterized by a high level of similarity in the diving profiles (Fig. 2). Data from periods 2 and 4 were pooled to compare them with those recorded in period 3 (asynchronous vs. synchronous periods, respectively). Period 3 lasted 7 hr 3 min, corresponding to 63 and 66% of the total time spent at sea during that day for A and B, respectively. The two penguins performed 57 and 59%, respectively, of the total number of dives during this synchronous phase.

Synchrony was observed during bouts marked not only by a foraging activity including either shallow or deep dives (Fig. 2, bottom panel), but also during bouts with no diving activity when birds were resting at the sea surface (Fig. 2, top panel). The transition between synchronous and asynchronous periods was sharply defined, the diving/resting patterns of birds A and B being quite different during phases 2 and 4 compared to phase 3 (Fig. 2, top and middle panels).

Time spent at the surface by the two penguins at the same time was significantly greater during the synchronous phase than during the asynchronous one (25.6% vs. 14.2%, t_1 = 25.1, $P < 0.001$). Similarly, time spent at the same depth (excluding the surface) at the same time was significantly higher during the synchronous phase (9.8% vs. 1.7%, t_1 = 4.14, $P <$ 0.001).

The mean vertical distance between the two birds at the same time was lower during the synchronous than during the asynchronous period (3.3 ± 3.5 vs. 8.7 ± 8.3 m, second-by-second analysis, t_{29512} = 64.2, $P <$ 0.001). Percentage distribution of the vertical distances between penguins was different during the two periods. Birds were at similar depths ($\leq$ 2 m) during 52% of the total diving duration of the synchronous period, but during only 16% of diving duration in the asynchronous phase. Ninety percent of underwater time was spent at a vertical distance $\leq$ 8 m between the two birds during the synchronous period and $\leq$ 22 m during the asynchronous phase.

When comparing dive characteristics during the two periods, the two penguins dove deeper (mean maximum depths: synchronous 15.5 ± 13.1 and 16.5 ±

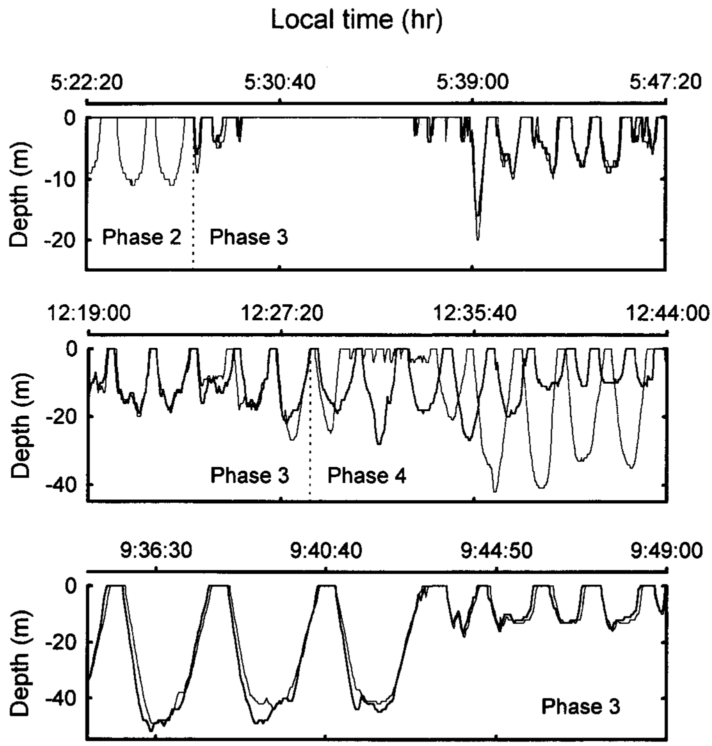

FIGURE 2. Record selected to illustrate various patterns in the dive records of the two birds. Top and middle: transition between the asynchronous and synchronous phases in the morning (top; phase 2 versus 3) and in early afternoon (middle; phase 3 versus 4). Bottom: a series of synchronous dives reaching deep and shallow depths. Time scale is different between bottom panel, and the top and middle panels. For phases 2 to 4 see text.

14.9 m vs. asynchronous 11.2 ± 9.6 and 9.0 ± 4.6 m for birds A and B, respectively, t_{513} = 4.3 and t_{502} = 8.3, *P*s < 0.001), longer (synchronous: 55.8 ± 37.7 and 55.5 ± 38.1 sec vs. asynchronous: 41.0 ± 26.5 and 37.7 ± 20.9 sec, for birds A and B, respectively, t_{513} = 5.2 and t_{502} = 6.8, *P*s < 0.001), and spent more time at the bottom of the dives during the synchronous phase than the asynchronous period (28.0 ± 20.5 and 28.9 ± 21.1 sec vs. 21.9 ± 14.7 and 20.8 ± 13.2 sec, for birds A and B, respectively, t_{513} = 3.9 and t_{502} = 5.3, *P*s < 0.001).

SYNCHRONOUS DIVING BEHAVIOR

During period 3, birds A and B performed 311 and 309 dives, respectively. The majority of these dives (*n* = 286, 92–93%) were synchronous, but the remainder (*n* = 23 and 25) were not. The few asynchronous dives were dissimilar, with either large differences in their diving and surfacing time and maximum depth reached, or one bird dove and the other did not. In comparison to synchronous dives, these asynchronous dives were more shallow (6.2 ± 4.0 and 4.9 ± 2.2 m vs. 16.3 ± 13.3 and 17.4 ± 15.1 m for birds A and B, respectively, t_{309} = 9.0 and t_{307} = 12.4, *P*s < 0.001) and of shorter duration (22.6 ± 18.4 and 17.6 ± 15.3 sec vs. 58.7 ± 37.5 and 58.5 ± 37.7 sec, t_{309} = 8.4 and t_{307} = 10.5, *P*s < 0.001). No statistical differences were found between the two birds when comparing the mean maximum depth and mean dive duration during either the asynchronous or the synchronous dives.

The majority (71%) of the 286 synchronous dives began with a time interval ≤ 4 sec between the two penguins, and 92% of the dives were initiated within 10 sec after the dive of one bird (Fig. 3). Synchronization in surfacing time was slightly less pronounced, 59% and 91% of the dives ending within 4 and 16 sec, respectively, after one bird had surfaced. The difference in duration of synchronous dives was low; it was ≤ 2 sec for 44% of the synchronous dives and ≤ 14 sec for 90% of them. The difference in maximum depth also was very low, 62% of the synchronous dives reaching maximum depths that differed from each other by 1 m or less, and 93% of synchronous dives occurring with a difference ≤ 6 m in maximum depth (Fig. 3).

TEMPORAL AND SPATIAL ORGANIZATION

Excluding data when birds were at the same depth at the same time, bird B spent significantly more time at greater depth than bird A during the synchronous phase (158 vs. 125 min for a total of 283 min; 56% vs. 44%). The two penguins reached different maximum depths during 214 (75%) of the 286 synchronous dives (Table 1). During these 214 dives, bird B dove

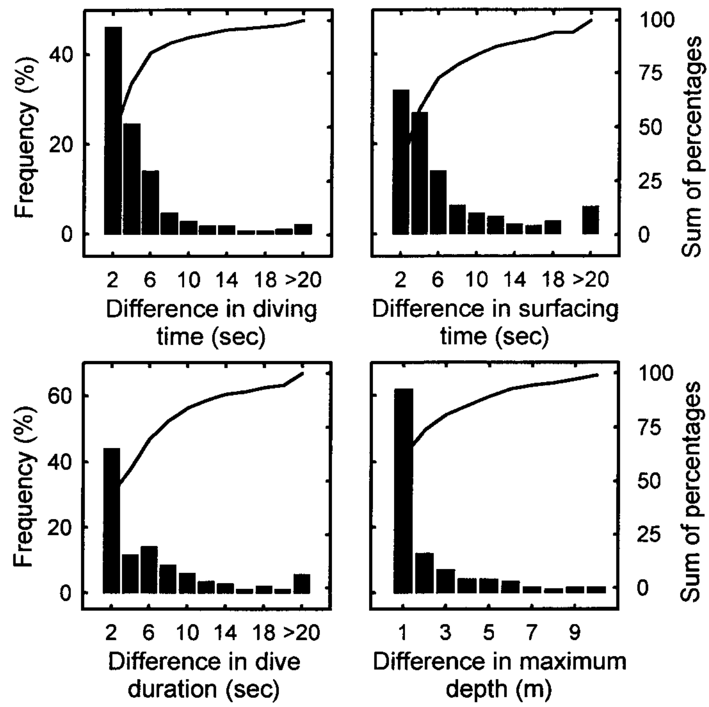

FIGURE 3. Comparison of diving parameters during all synchronous dives (n = 286) of the two birds: frequency of the difference in time when birds initiate and end each dive, and difference in total dive duration and in the maximum depth reached for each synchronous dive.

deeper in a greater number of dives than bird A (57% vs. 43%, χ^2_1 = 4.79, $P < 0.05$). The distribution of maximum depths of synchronous dives (calculated as the mean between each pair of synchronous dives) was bimodal, with 215 (75%) of dives reaching depths ≤ 25 m (shallow dives) and 71 dives (25%) being deeper (deep dives). During shallow dives, penguin A dove more often deeper than penguin B (61% versus 39%, respectively, χ^2_1 = 7.11, $P < 0.01$), whereas bird B reached deeper depths in most of the deep dives (96% versus 4%, χ^2_1 = 58.5, $P < 0.001$).

Overall, penguin B initiated (78% versus 22%, χ^2_1 = 80.6, $P < 0.001$) and ended (71% versus 29%, χ^2_1 = 46.5, $P < 0.001$) most of the synchronous dives, including both shallow and deep dives (Table 1). The bird which initiated the dive was generally the bird which ended it first (n = 169 for a total of 261, 65%), but it dove shallower than the other penguin (n = 104, 40%).

MEAL MASS AND DIET COMPOSITION

Stomach contents weighed 193 and 158 g for birds A and B, respectively. In both samples, crustaceans

TABLE 1. Synchronization of diving behavior within penguins A and B.

	All dives		Shallow dives (≤25 m)		Deep dives (>25 m)	
	n	%	*n*	%	*n*	%
Bird A dived first	58	20.3	49	22.8	9	12.7
Bird B dived first	203	71.0	148	68.8	55	77.5
Birds dived at the same time	25	8.7	18	8.4	7	9.9
Bird A surfaced first	79	27.6	61	28.4	18	25.4
Bird B surfaced first	191	66.8	138	64.2	53	74.6
Birds surfaced at the same time	16	5.6	16	7.4	0	0.0
Bird A dived deeper	91	31.8	88	40.9	3	4.2
Bird B dived deeper	123	43.0	56	26.1	67	94.4
Birds dived to the same maximum depth	72	25.2	71	33.0	1	1.4
n	286		215		71	

formed the bulk of the diet by mass (90.9% and 90.2% of contents for A and B, respectively) and by number (99.4% and 99.2%) with only one prey species involved, the euphausiid *Thysanoessa gregaria.* Fish and squid were a minor part of the diet both by mass (3.4% and 0.6% for fish, and 5.7% and 9.2% for squid in samples for A and B, respectively) and by number (0.5% and 0.4% for fish, and 0.1% and 0.4% for squid), with the same two different taxa of fish and squid occurring in the two samples.

DISCUSSION

To our knowledge, this study is the first to investigate synchronous underwater foraging behavior in penguins. The only explanation of the identical diving records is that the two females of Northern Rockhopper Penguins dove and surfaced together, and were visually in contact during seven consecutive hours at sea, which suggests a coordinated underwater behavior to catch prey. The birds also spent similar amounts of time together at the surface, either resting during a long bout or recovering from diving activity between two consecutive dives. In agreement with communal foraging behavior, qualitative and quantitative analysis of stomach contents showed that both penguins fed on the same prey, the euphausiid crustacean *Thysanoessa gregaria.*

The discrepancy between the numerous visual observations of penguins in groups at the sea-surface and the lack of information on their underwater behavior is due to the low probability of obtaining synchronous dive records using electronic devices. Penguins generally live in large and dense colonies and only a few birds can be equipped on the same day with costly time-depth recorders, thus greatly increasing the dilution effect of colony size. Northern Rockhopper Penguins used in this study were located in the same area of a small colony (about 200 pairs) at a time when females performed short foraging trips. Even under these relatively favorable conditions, the probability of recording synchronous diving activity of at least two birds is low.

This work complements previous visual observations of penguins swimming and moving in and out of the water in flocks (Siegfried et al. 1975, Broni 1985, Wilson and Wilson 1990). A relatively short time separated the two Rockhopper Penguins when they dove and surfaced (Fig. 3), such as has been recorded in groups of African Penguins *Spheniscus demersus* (Siegfried et al. 1975, Wilson et al. 1986). Slight asynchrony in the time of diving and surfacing was only observed in groups of more than 12 of these birds (Wilson et al. 1986). This, together with the fact that penguins of the genus *Eudyptes* are generally observed at sea in small flocks (< 20–30 birds) (Marchant and Higgins 1990, unpubl. data), makes it likely that the two equipped birds were part of a larger group of foraging penguins.

Birds A and B departed from and returned to the colony independently, and their behavior at sea was not synchronous at the beginning and the end of the foraging trip. The penguins thus met up and then separated again at sea. This behavior is in agreement with the view that small penguin groups encountered in foraging areas are parts of much larger groups that coalesce when food sources are found (Davies 1956, cited in Broni 1985).

Rockhopper Penguins mainly feed on euphausiid crustaceans and myctophid fish (Cooper et al. 1990) which are known to occur in dense aggregations (Mauchline 1980, Kozlov 1995). At Amsterdam Island, the two most abundant prey of the Rockhopper Penguins during the chick rearing period are the euphausiids *T. gregaria* and *Nematoscelis megalops* (Tremblay et al. 1997). Accordingly, the stomach contents of birds A and B contained, respectively, about 10,800 and 8,300 individual *T. gregaria* at the end of their daily foraging trip. Both *T. gregaria* and *N. megalops* are known to occur in great swarms where predators concentrate (Lomakina 1966, Mauchline 1980). Because the benefits of communal foraging increases with the patchiness and abundance of food at patches (Pulliam and Caraco 1984), Rockhopper Penguins are likely to profit by foraging in groups on swarming euphausiids.

When a food patch is located, individual penguins may either hunt independently or cooperate. The fact that the diving profiles were identical during the descent and ascent phases, and also during the bottom (feeding) time (Fig. 3), supports cooperative foraging. Cooperative foraging has been reported for African Penguins, which feed by circling fish schools and capturing prey when the school is depolarized, thus reducing the antipredator coordinated behavior of the prey (Wilson et al. 1987, Wilson and Wilson 1990). The close similarity in the time-depth profiles also indicates that birds A and B were visually in contact during the dives, allowing them to change their underwater behavior at the same time (Fig. 2). Whereas ambient light levels decrease with depth, Rockhopper Penguins were still in contact until at least 60 m, the deepest synchronous recorded dive reaching that depth (Fig. 1). The main visual cue was probably the conspicuous black and white patterned plumage of penguins. This pattern may have been selected to assist in prey capture (Cairns 1986, Wilson and Wilson 1990), but also may serve to maintain group cohesion.

While diving in synchrony, some slight differences were found between the two birds in the maximum depth of synchronous dives, their duration, and the time of diving and surfacing (Fig. 3). These differences were not randomly distributed among birds (Table 1). At the sea-surface, behavioral variations among individuals have been found in the African Penguins for which a time-lag similar to that observed in Rockhopper Penguins (Fig. 3) was noted between diving by the birds on the perimeter of the group and those in the center (Broni 1985).

In conclusion, this study shows that penguins are able to dive in synchrony during several consecutive hours and suggests that cooperative underwater feeding activity is part of their foraging repertoire.

We thank Jean-Yves Georges and Eric Guinard for collecting data in the field, and David Ainley, Henri Weimerskirch, and Rory Wilson for their helpful comments. This work was supported financially and logistically by the Institut Français pour la Recherche et la

Technologie Polaires and the Terres Australes et Antarctiques Françaises.

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