Sex-specific foraging behaviour in a seabird with reversed sexual dimorphism, the red-footed booby

Henri Weimerskirch [1*], Matthieu Le Corre [2], Yan Ropert-Coudert[3], Akiko Kato[3] & Francis Marsac [1]

[1] IRD, Centre de la Réunion, UR 109 Thetis, BP 172, 97492 Sainte Clotilde, Ile de la Réunion, France
[2] Laboratoire d'Ecologie Marine, Université de la Réunion 15 avenue René Cassin, BP 7151, 97715 Saint Denis, Ile de la Réunion, France
[3]National Institute of Polar Research, 1-9-10 Kaga, Itabashi-ku Tokyo 173-8515 Japan

* Email : henri.weimerskirch@la-reunion.ird.fr

Abstract

Most hypothesis attempting to explain the evolution of reversed sexual dimorphism (RSD) assume that size-related differences in foraging ability are of prime importance but the studies on sex specific differences in foraging behaviour remain scarce. We compare the foraging behaviour of males and females in a seabird species with a reverse sexual dimorphism by using several miniaturised activity and telemetry loggers. In red-footed boobies males are 5% smaller and 15% lighter than females. Both sexes spent similar time on the nest while incubating or brooding. When foraging at sea, males and females spent similar time foraging in oceanic waters, forage in similar areas, spent similar proportion of their foraging trip in flight, and feed on similar prey of similar size. However flight speeds and the depths attained were slightly higher for females than in males. More importantly, compared to males, females ranged farther during incubation (85 km versus 50 km) and furthermore fed mostly at the extremity of their foraging trip, whereas males actively foraged throughout the trip and were much more active than females, landing and diving more often. Males tended to feed overall on larger proportion of squids than females. During the study period, males lost mass, whereas females showed no significant changes. These results indicate that males and females red-footed differ in several aspects in their foraging behaviour. Although some differences may be the direct result of the larger size of females, i.e. the slightly higher speeds and deeper depths attained, others indicate clearly different foraging strategies between the sexes. The smaller size of males may thus be advantageous in conferring them a higher agility, and to occupy a foraging niche different from that of females. The higher foraging effort of males related to its different foraging strategy is probably at the origin of the rapid mass loss of males during the breeding period. This suggests that foraging differences are probably the reason for the differential breeding investment observed in boobies, and are likely to be involved in the evolution and maintenance of RSD.

INTRODUCTION

In birds, mammals and reptiles, males are generally larger than females (Andersson 1994). The greater body size of males is most commonly attributed to sexual selection acting on males, i.e. as the outcome of evolutionary increases in body size of males as a result of competition for access to females (Promislow et al. 1992, Andersson 1994). Reverse sexual dimorphism (RSD, females are larger than males) occurs in a number of groups, and is well known in several bird families, raptors, owls, jacanas, phalaropes, skuas and jaegers, boobies and frigatebirds. Whereas in some groups such as jacanas or phalaropes sex roles are reversed and RSD is also attributed to sexual selection, in the other groups where species are all monogamous there is no sex-role reversal. The origin and maintenance of RSD in these groups has been the subject of much debate, and no definitive answer has been proposed (Mueller 1990). The larger size of the female may be selectively advantageous in several ways and the processes that lead to dimorphism may act on either sex and larger or smaller size may be advantageous in terms of behaviour and dominance for access to females (or to resources), but also in terms of energetic (production of eggs, starvation capabilities, mobility or foraging costs for example), or in terms of breeding investment, or in a combination of these (Shine 1989). The main divergence between hypotheses is related to whether they try to explain the evolution of large female or small males (e.g. see review in Massemin et al. 2000) but of course different hypothesis or a combination of hypotheses may apply to the different groups where RSD occurs. One of the most popular hypothesis, the ‘division of labour’ hypothesis, suggests that size dimorphism is an adaptive consequence of different roles and has received support in the best studied groups, raptors and owls, where selection may result in large females that incubate and guard the nest, and in small males that forage on agile prey (Newton 1979, Lundberg 1986). Although most hypothesis attempting to explain the evolution of RSD assume that size-related differences in foraging ability are of prime importance, the evidence remains scarce (Mueller 1990) because of the difficulty to study directly the foraging behaviour of birds.

In seabirds, males and females share generally equally the breeding duties, the sexes are generally similar in external appearance, except in frigatebirds, and sexual size dimorphism is overall not extensive. Typical sexual dimorphism (males larger than females) is much more common than RSD (Fairbairn & Shine 1993). Several studies have examined differences in foraging behaviour between the sexes in species where males were larger than females and found important differences that are generally supposed to be mediated by the difference in size (see review in Lewis et al. 2002). Some studies have however found differences between males and females in provisioning behaviour or foraging behaviour of monomorphic species (see review in Lewis et al. 2002), suggesting that the foraging differences found in sex dimorphic species may have not only been mediated by differences in size, but also by other constraints, such as those related to breeding energetics. To examine further the possible role of sex specific differences in foraging in the evolution of size differences in seabirds information on seabird groups with extensive RSD are necessary (Fairbairn & Shine 1993). In frigatebirds, where size difference is maximum among seabirds, males and females differ extensively in their kleptoparasitic foraging behaviour (Harrington et al. 1972, Gilardi 1994, Lagarde et al. 2001), and males stop provisioning the chick before the end of the chick-rearing period (Osorno 1999). However it is not clear how differences in foraging relate to the evolution of RSD in frigatebirds where males are involved in complex displays to attract females and sexual selection is likely to have played in important role in the evolution of RSD (Nelson 1981, 1983). In skuas and jaegers that are also kleptoparasitic and powerful predators of other seabird RSD is generally attributed to sexual selection (Catry et al. 1999). Thus in seabirds with RSD, two groups have a raptorial lifestyle similar to owls or raptors and it generally assumed that RSD is related to the morphology or ecology of avian predators, regardless of its evolutionary origin in other taxa (Catry et al. 1999).

Thus boobies appear as an interesting group to study the evolution of RSD among seabirds because they appear as more typical seabirds than the two other groups. In boobies it has been suggested that ‘division of labour’ is minimal (Guerra & Drummond 1995, Lormée et al. in press), although females provision the large chick in a larger extent than males (Anderson & Ricklefs 1992, Guerra & Drummond 1995, Simmons 1970, Tershy & Croll 2000), possibly at least in part as a simple result of their larger size. Several studies have suggested that male boobies could be more energetically constrained than females that could have a more flexible breeding effort because their large size allow them to buffer more easily periods of food stress (Velando & Alonso-Alvarez 2003) and invest more in the offspring provisioning (Anderson & Ricklefs 1992, Guerra & Drummond 1995). As a result, in contrast with most seabirds that share equally breeding duties in boobies males may invest less in reproduction than females, at least during chick rearing. Such differences may result from differences in foraging behaviour between the sexes and the origin of RSD in these species might be linked to a partition of foraging niches to optimise foraging profitability of both sexes (Selander 1966, Fairbairn & Shine 1993). For example the larger and heavier females may plunge to greater depths than males (Simmons 1970, Nelson 1978), or may forage at different distances from the colony or in different areas (Gilardi 1992). Selection on females for increased chick provisioning may have lead to increased size and foraging range, males being selected to remain close to the colony to maintain territories and prevent or acquire extra pair copulations, thus reducing foraging range and body size (Gilardi 1992). These studies underline the necessity to consider the possibility of differences in foraging behaviour in species with RSD, together with the energetic constraints of foraging and breeding. Until now no study has examined whether sex specific differences in the foraging behaviour at sea of breeding birds exist in species with RSD, apart from the studies on the specific kleptoparatic behaviour of frigatebirds, and how they relate to breeding investment. With the development of miniaturised loggers and telemetry systems (e.g. Weimerskirch et al. 2002), it is now possible to study this question on free-ranging animals in the open sea..

The red footed boobies (*Sula sula*) is particularly interesting to examine this question because it is the only booby, with the rare Abbot's booby, with a one egg clutch, extremely long period of parental care, and most pelagic lifestyle (Nelson 1978). The two sexes regulate their body reserves differently (Lormée et al. 2003), and females provision the large chick more than males, and infrequently compared to other boobies (Lormée et al. in press). If differences in foraging behaviour exist, they may be the most apparent in the species where foraging constraints are high, i.e. in species foraging far from colonies, and provisioning their chick infrequently. The aim of the study is to examine whether the foraging behaviour of red footed boobies differs between the sexes. To examine this, we have used a series of miniaturised loggers and telemetry systems to study the foraging behaviour of male and females breeding on Europa Island in the Mozambique Channel.

MATERIAL AND METHODS

The study was carried out on Europa Island (22.3° S, 40.3°E), in the Mozambique Channel between 18 August and 30 September 2003. The population of red-footed boobies breeding on Europa is about 2800 to 3800 pairs, with all colonies located in the dry *Euphorbia stenoclada* forest of the northern part of the island (Le Corre & Jouventin 1997). Red-footed boobies are seasonal breeders at Europa with most egg-laying occurring between July and October each year (Le Corre 2001). Thus during the course of our study most pairs were incubating or brooding young chicks. Red-footed boobies show several plumage morph that change extensively according to localities (Nelson 1978). In the Indian Ocean most extant colonies hold birds of the white morph, except at Europa where 98.5% of the birds are of the white-tailed brown morph, and 1.5% of the white morph (Le Corre 1999). At first capture, each bird was ringed, measured (culmen length with a caliper, wing length with a ruler) and weighed in a bag using a Pesola balance. Body condition was calculated as the residual mass from a linear regression relating body mass to wing length (Wing length = 4.8061 Mass - 925.1, R^2=0.3175, P<0.001). They were sexed by voice (when captured, males have a higher pitched voice than females, Nelson 1978, Lormée et al. 2000), and by measurements (within a pair, females are larger than males). Sexing by voice and measurements was controlled by molecular sexing on a sub-sample of 15 individuals: all sexes assigned by voice and measurements were confirmed by molecular sexing (see Lormée et al. 2000 for details of the molecular method of sexing used).

Our main study plot included about 50 nests built on trees at 1 to 6 meters from the ground. At the beginning of the study period, each nest was numbered with a plastic tag and the colony mapped, and on each nest one bird within the pair was marked using a sprayer with a yellow patch of picric acid on the white tail and thus without handling the birds. This yellow patch allowed us to identify rapidly birds at a distance. The study colony was monitored 3-4 time per day (at dawn and dusk, i.e. at 6h00 and 17h45, and one or two times in the middle of the day) to control for the presence of adults on the nest and thus to infer the duration of foraging trips and departure and return of birds fitted with loggers. Thereafter birds were captured for the purpose of attaching loggers. They were captured by hand for those accessible from the ground, or with a 6 meters telescopic fishing pole fitted with a nylon noose for the birds nesting higher on the trees. When captured for the first time, birds were measured (culmen length, beak width and maximum height, wing length), weighed and banded with a stainless steel band. When recaptured for logger recovery, they were only weighed.

To study the horizontal movements of boobies 16 birds were fitted for 2 to 5 successive foraging trips (46 foraging trips in total) with PTT 100 satellite transmitters (Microwave telemetry, Columbia, MA, USA) weighing 20 g. In addition we fitted 16 different individuals with a GPS receiver with integrated antenna and a 1-Mbyte flash memory operated by a rechargeable battery (Newbehavior; Zürich, Switzerland, Steiner et al. 2000) recording at 10 sec intervals. The loggers were sealed into small polyethylene bags, the overall weight of the device and its waterproof package was 32 g.

To study the activity patterns of boobies, we equipped 22 birds for 1-5 successive foraging trips with 6 g activity recorders (IMV2, Immersion Monitor Version 2, Ferguson Manufacturing, Winston Salem, NC, USA) that record the presence of sea water across its electrodes to infer the time the device was immerged in sea water and the time it is dry. Fitted on a metal band with Tape, it allowed us to measure precisely the timing of landing or diving on water and of take offs, and thus the duration of bouts spent on the water, or in flight.

To study the flight behaviour and dive depths we used cylindrical accelerometers – time depth four-channel data loggers (M190-D2GT, 12 bit resolution, 60x15 mm, 20 g, Little Leonardo, Tokyo, Japan) on 12 birds for 1-2 trips. The devices simultaneously monitored depth (every one second), temperature (every minute) and acceleration (16 Hz) along two axes. The units contain a tilt sensor capable of measuring both dynamic acceleration (e.g. vibration) and static acceleration (e.g. gravity). Loggers were attached to the birds' tails so that acceleration was measured along the following two axes: surging acceleration measured along the longitudinal body axis of the birds and the heaving acceleration measured dorso-ventrally (Fig. 1, Watanuki et al. 2003; see also Ropert-Coudert et al. 2004a, b). The absolute accuracy for the depth sensor was 0.1 m.

PTTs, GPS and accelerometers were taped under the three central tail feathers using Tesa© tape and activity recorders were placed on the tarsus, taped on a metal band. Because red-footed boobies are relatively small seabirds (mass 780 –1050 g), only one type of logger was fitted on each bird (representing a maximum – for GPS – of 3-4% of the bird body mass for the GPS) except for activity recorders that were deployed together with PTTs to 12 individuals (2.5-3.3% of the bird body mass in total) to derive the location of landings.

The locations obtained by the Argos system were filtered following Weimerskirch et al. 1993, with a maximum flight speed of 95 km h^{-1} for red-footed boobies, based on the recording of GPS (see results). Data were treated using a custom software package ('Diomedea', D. Filippi, see Weimerskirch *et al*. 2000 for details and other examples of its usage). This software takes into account the time spent on the water and in flight by activity logger-equipped birds, so that the real mean speed of travel between successive satellite locations can be estimated. It calculates a location every 10 sec so that data of GPS and of satellite tracking can be pooled for the estimates of foraging areas. For GPS, satellites were lost during some sections of the trips, and therefore these sections were not considered in the analysis. The locations of the active foraging were derived from the periods when the birds were sitting on the water as recorded by the activity recorders fitted with PTTs, or for speeds lower than 10 km h^{-1} for the GPS recording (see results). To estimate the foraging areas of boobies we used kernel estimation techniques to delineate the foraging ranges and the core habitat areas used by boobies fitted with satellite transmitters and GPS. We first pooled the location obtained from the GPS and the PTTs. We used the fixed kernel method (Worton 1995) and the least square algorithm (Seaman & Powell 1996). For estimations of surface foraged, we used the fixed kernel estimate of 95% home range area (Seaman & Powell 1996): we calculated the percentage of overlap of the 95% home range area of males and females only during incubation, because during brooding the sample size was too sample for meaningful kernel estimates. For mapping purpose we plotted the overall range and estimated contours levels including for 50 % (core area) and 95% of the locations distribution (Wood et al. 2000, Hyrenbach et al. 2002). The sinuosity of flight tracks measured by GPS was calculated as the ratio of the actual distance covered to the straight-line distance between every sixth fix, i.e. every 60 sec. A value of one indicates a straight line.

Food samples were collected from breeding adults caught on their nest, while incubating or brooding a chick. Food samples were frozen and returned to our lab for analysis. In the laboratory, each sample was weighed; items were then separated from each other and weighed separately. Birds sometimes regurgitated large numbers of cephalopod beaks, which had accumulated in the gizzard. Fresh prey items were washed with water and separated from accumulated ones. Identification of prey was made using Smith and Heemstra (1986) for fishes, Clarke (1986) and Nesis (1987) for squids, 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 squids. We used allometric relationships (see Le Corre et al. 2003) to reconstitute mass and length of partially digested items of the 3 main groups of preys (the fishes Exocetidae and Hemiramphidae and the squids Ommastrephidae). The accumulated beaks of squids 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 allometric equations.

Statistical analyses were performed with STATISTICA 6.0. Average values are given with ± one standard deviation. Because the individuals were tracked for several successive trips, to avoid pseudoreplication problems we analysed the data on the characteristics of the trips using mixed-model ANOVAs. Speed, range, distance covered, activity etc… were the dependent variables, categories (sex, period, stage etc…) were entered as fixed factors and individual was considered as a random factor. Values for variables representing percentage were arcsine transformed before performing ANOVAs.

RESULTS

Size, body condition, time spent on nest and foraging

Females were 14.8 % heavier and 4-6% larger than males (Table 1). During the course of the study, the body condition of both females and males tended to decline, but only males at a significant rate, almost four times higher than that of females (Fig. 1; Females: y=71.6-1.28x, R^2=0.0591, P=0.09; males y=40.6-4.5x, R^2=0.406, P<0.001).

Both sexes were observed incubating or brooding chicks during the day as frequently (χ^1_2=0.08, P=0.987 and χ^2_1=0.89, P=0.645 respectively, Table 2). The duration of foraging trips (Table 2) was similar for males and females during incubation (Mixed ANOVA, $F_{1,28}$=1.5, P=0.235) and during brooding ($F_{1.12}$=0.87, P=0.377).

Flight speed and flight pattern

Speeds measured at 10 sec intervals with GPS showed a bi-modal distribution, with speeds lower than 10 km h^{-1} corresponding to birds on the water or diving and speeds higher than 10 km h^{-1} to birds travelling (Fig. 2). Median flight speed was 40.5 km h^{-1} for females, and 34.8 km h^{-1} for males, with a slightly different distribution between the sexes (Fig. 2), but the average travelling speeds were not significantly different between the sexes (Table 2, Mixed ANOVA, $F_{1,14}$= 1.3, P=0.264).

When travelling, red-footed boobies alternate flapping and gliding bouts. The percentage of time spent flapping was similar between males and females (Mixed ANOVA, $F_{1,6}$= 0.43, P=0.535; Table 2). The overall sinuosity of flight tracks was similar between males and females (Mixed ANOVA, $F_{1,14}$=0.33, P=0.573, Table 2).

Foraging movements and foraging zones

During the foraging trips boobies are doing either return trips where the birds are going straight to a particular area at the extremity of the trip, with the route on the outward part being parallel to the route on the return part, or looping movements (Fig. 3). Only 17.4% of females trips had a loop shape whereas 46.1 % of male tracks had a looping movement (χ^1_2=5.4, P=0.02). Females had on average a longer maximum foraging range compared to males during the incubation period, but not during the brooding period (Table 2, Mixed ANOVA $F_{1,14}$=8.08, P=0.0122 and $F_{1,9}$=0.95, P=0.631 respectively).

Birds alternated periods in flight travelling and periods of active foraging, spending time on the water or diving (Fig. 3). The location of periods on the water were determined by the activity recorders combined with satellite transmitters that indicated sea landings, or directly by flight speeds of GPS lower than 10 km/h. During incubation, zones of active foraging tended to be located at the extremity of the foraging trips in females (75% of foraging time was located at 80% or more of the maximum range), whereas males spent a significant amount of time foraging actively throughout the foraging trip (42% at 80% or more of foraging trip). During brooding distributions were similar (Fig. 4).

The overall foraging area of females was larger than that of males (6535 km^2 versus 4372 km^2, Fig. 5). During incubation 64.9% of the 95% core of males was overlapped by the 95% area of female, whereas only 29.5% of the area of females was covered by males (Fig. 5).

Activity and diving

Since there was no significant effect of the stage (incubation or brooding), on the activity parameters data for the two sexes were pooled. Males and females spent similar amounts of time in flight (Table 2, Mixed ANOVA, $F_{1,30}$=0.46, P=0.503), and spent similar durations of bouts in flight and on the water ($F_{1,13}$=2.2, P=0.165, $F_{1,13}$=2.8, P=0.122 respectively). However males landed more often than females (Table 2, $F_{1,13}$=11.3, P=0.0017).

Males dived more frequently at depths lower than 10 cm than females (Table 2, Mixed ANOVA $F_{1,8}$=6.1, P=0.044), either through plunge diving or surface diving. There was no difference between males and females in the proportion of dive type used (3.6±3.8 % of surface dives versus 5.6±12.1 respectively, Mixed ANOVA $F_{1,8}$=0.112, P=0.739). The distribution of diving depths was slightly different between the sexes, deeper depths being more common in females than in males, and shallower depths in males (Fig. 6). During plunge dives males and females attained similar maximum depths (Table 2, $F_{1,8}$=1.67, P=0.240) and similar durations of dives (Table 2, Mixed ANOVA, $F_{1,8}$=2.03, P=0.202).

Diet

The mass of food loads and the number of prey in each food load were similar for males and females (58.6±40.9g, n=25 and 63.6±54.3g, n=34 respectively, $F_{1,57}$=0.153, P=0.69; 4.4±3.9 preys per stomach and 4.7±3.4 respectively, $F_{1,57}$=0.11, P=0.74). Red-footed boobies prey mainly on flying fishes and flying squids (Ommastraphidae). Fishes and squids were found in similar proportions in males and females (41.9 % of fishes in males, 45.3 % in females, (χ^2_1=0.035, P=0.85), but fishes represented a higher total mass for females than for males (74.6 versus 59.2 % of the total mass of food samples combined, χ^2_1=94.17, P<0.01).

There was a tendency for males and females to prey on different proportions of prey families, but the difference was not significant (χ^2_2 = 9.33, p=0.09, Table 3a). The size and mass of the major prey were not different between males and females (Table 3b).

DISCUSSION

Foraging differences

Although males and females red-footed boobies spend similar time incubating or brooding the young chick at the colony, and similar time foraging at sea, significant differences exist between the two sexes in their foraging behaviour. Female red-footed boobies are larger and heavier than males and the slight differences observed between the two sexes for some foraging parameters could be the result of the size differences only. The larger size may account for the slightly higher travelling speeds of females, since flight speed is size and mass dependent (Pennycuick 1989). Similarly because plunge divers use the momentum of the plunge to gain depths (Ropert-Coudert et al. 2004a) the slightly deeper depths attained by females may be simply the result of their larger size. Smaller size is expected to also result in reduced foraging costs, and therefore in a longer foraging range as found in owls for example (Sunde et al. 2003), but this was not the case in red-footed boobies.

The other differences in foraging found between males and females are probably not the result of size differences only. As suspected for brown boobies (Gilardi 1992) and other boobies (Nelson 1978) but never demonstrated, the larger females appear to have a longer foraging range and area covered than males. Since foraging times and time spent at sea are similar and the differences in speeds between sexes are very limited, this means that males are spending more time foraging in particular sites. Males appear to have a different way of foraging to that of females. While females head to a particular direction and forage actively at the extremity of their trip, males appear to forage actively much more frequently en route, on the outward part, at the extremity as well as on the return part of the trip. As a result ptobably the shape of tracks differs between the sexes. More active foraging is also shown by the higher number of sea landings per hour and higher number of dives per hour. Different activity budgets and foraging pattern probably result from different ways of foraging between males and females, allowing niche partitioning. Although diets appear to be similar, the higher proportion of squid in males may be related to differences in foraging strategies. Boobies are known to rely extensively in their association with sub-surface predators such as tuna or dolphins (Au & Pitman 1986, Ballance et al.1997), and the differences in foraging strategy may be related to different association strategies, with specialisations toward a particular sub-surface group, or toward association versus non-association for example.

In seabirds RSD is found mainly in tropical species (Fairbairn & Shine 1993). In tropical waters, the low productivity and more patchy distribution of prey patches, together with more elusive prey caught such as flying fishes and flying squids, may have favoured the selection of specific foraging strategies including proficient flight associated with surface –or near surface feeding (Ainley & Boekelheide 1983, Ballance & Pitman 1999). Frigatebirds and boobies appear to have developed foraging strategies with low costs of foraging and specific foraging techniques (Ballance 1995, Weimerskirch et al. 2003, in press, in prep). Within a particular species for which it has been suggested that flight strategy is based on a reduction of flight costs (Ballance 1995), important differences appear to have been selected between the sexes. The specific foraging technique used by male boobies with a much higher activity might be obviously favoured by a smaller size in terms of manoeuvrability and efficiency (lowered flight costs). The increased foraging costs due to active foraging strategy of males may be tempered by the smaller size. Similarly to raptors and owls may more likely be advantageous for aerial agility during foraging (Jehl & Murray 1986, Lundberg 1986). Hence smaller size by males in boobies may fit the 'foraging profitability' pattern observed in raptors where small size confer a better ability to catch agile prey (Wheeler & Greenwood 1983). However the possible selective advantage provided by the smaller size of males boobies and raptors is not associated in boobies with a division of labour between the sexes since males participate similarly to females to incubation and brooding.

Breeding investment and foraging

In boobies, females provision large chicks in a much larger proportion than males, whereas during incubation and early brood stage no difference between sexes is found in nest attendance, foraging trip duration and provisioning (Guerra & Drummond 1995, Tershy & Croll 2000, Lormée et al. in press). Studies carried out on provisioning of large chicks suggest that reversed size dimorphism of blue-footed boobies is unlikely to be an adaptive result of different roles of the sexes in parental care; rather dimorphism appears to be the cause of unequal feeding contributions by males and females (Guerra & Drummond 1995, Velando & Alonso-Alvarez 2003).

Our study took place during the incubation period and early brooding stage, i.e. when males and females do not differ in nest attendance or provisioning in boobies (Guerra &

Drummond 1995, Lormée et al. in press, this study). At this stage one would not expect that differences in foraging strategy differ, since the birds do no differ in nest attendance and breeding investment, if the foraging pattern was the consequence of breeding investment? However, our study shows that although time spent foraging and attending the nest are similar, males are loosing body mass throughout the period, whereas females do not significantly loose mass. This means that incubation and early brooding are more constraining for males. Two reasons, not exclusive may explain this. Because of their smaller size, and similar nest attendance, males are less suited to sustain fast on the nest. But our study shows also that foraging costs are higher for males as a result of higher effort. The higher number of take offs, that are known to represent a significant part of the foraging costs in flying birds (Weimerskirch et al. 2000) probably results in higher energy expenditure.

Thus males are less efficient than females during incubation and early brooding as a result of their different foraging strategies. The resulting mass loss of males brings them with a poor body condition at the beginning of the chick-rearing period, whereas females have more fat stores than males. This probably explains the patterns observed in several species of boobies where females are able to provision their chick in a larger extent than males (Guerra & Drummond 1995, Lormée et al. in press) and especially the inability of males boobies to regulate provisioning (Velando & Alonso-Alvarez 2003). These authors suggested that male boobies provisioning chicks have a fixed body mass and are working at a physiological maximum. Our study suggest that because of higher foraging costs due to different technique, males are using their body reserves early in the breeding seasons, and have no safety margin that would allow them to regulate provisioning (Weimerskirch 1999).

The evolution of RSD – adding the foraging component in the picture

In species with RSD, dimorphism is present in many traits and selection has therefore been presumed to act non independently on several characters (Lande and Arnold 1983), and RSD has been discussed mainly in terms of differences in body size (Mueller 1990). Many hypotheses have been proposed to explain the evolution of RSD in birds, but different hypothesis might apply for different groups. Studies have focused mainly on raptors or owls (e.g. Wheeler & Greenwood 1983, Newton 1979, Lundberg 1986), and much less on other groups, especially on seabirds (Jehl & Murray 1986, Fairbairn & Shine 1993). Seabirds are interesting because males and females generally share equally the breeding duties, and thus hypothesis that larger size is advantageous for females for egg production and maternal investment put forward in raptors for example does not hold. However within seabird with

RSD two groups can be separated. In species with a raptorial life style, frigatebirds, jaegers and skuas, it is likely that sexual selection operates (see Catry et al. 1999 for skuas and Jaegers), especially in frigatebirds that have an extravagant sexual attributes displayed by males (Nelson 1981, 1983). Differently from raptors, in these species males and females share equally much of incubation and brooding, and only in frigatebird the species with the highest dimorphism females take care solely of chicks during the later stages of the fledging period (Osorno 1999). In frigatebirds, several studies have shown that kleptoparasitic behaviour differs greatly between the sexes (Harrington et al. 1972, Gilardi 1992, Lagarde et al. 2001) whereas in skuas and jaegers no difference in foraging was found between the sexes (Catry et al. 1999).

The raptorial lifestyle of kleptoparasitic species produces confounding effects when trying to understand the adaptive significance of RSD in seabirds. Boobies are more typical seabirds than the two other seabird groups with RSD and are more comparable to other seabird species. Red-footed boobies present specific adaptations to foraging in low productivity tropical environment and males and females differ in foraging strategies. Foraging in tropical waters, or at least in waters with low productivity waters, appear to correlate in some extent with the appearance of RSD (Fairbairn & Shine 1993). In the closely related monomorphic gannet breeding in temperate waters differences in foraging behaviour between males and females do occur (Lewis et al. 2002). In tropical waters smaller size may be advantageous to lower costs for catching more elusive preys such as flying fishes. The advantage of the larger size of females may be related to the energetic of breeding. Our study clearly shows that foraging strategies differ between sexes, and not only as a consequence of differences in size. The differences in foraging allow us to understand the consequence in terms of breeding investment, higher foraging effort resulting in higher body mass loss and thus in lower relative, and absolute, investment in the chick by males. However the pattern observed does not allow us to decide whether the differences observed are the cause for the evolution of RSD, or the consequences of an other trait that would have been selected. Further comparative work within families with RSD, and between families with RSD and typical sexual dimorphism on the ecological consequences of different body sizes and different degrees of dimorphism should allow us to better understand the adaptive significance of RSD.

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Table 1 – Mass and measurements of males and females red-footed boobies from Europa Island.

	Males	Females	t test
Culmen length (mm)	81.8 ± 3.3 (75-91) (33)	84.8 ± 2.6 (78.5-90) (43)	t=4.3, P<0.0001
Culmen height (mm)	27.0±1.2 (24-29.7) (31)	28.7±1.4 (25.5-32) (38)	t=5.3, P<0.0001
Culmen breadth (mm)	22.5±1.1 (20.5-25)(31)	23.2±0.9 (20.5-25)(36)	t=2.6, P=0.013
Wing length (mm)	383.9±7.7 (363-400) (31)	394.1±8.9 (378-412)(36)	t=5.3, P<0.0001
Weight (g)	891.2±64.4 (780-1060)(34)	1020.4±50.1 (940-1140) (46)	t=9.9, P<0.0001

Table 2 – Nest attendance and foraging parameters of males and females (average ± one standard deviation, sample size and range)

	Males	Females	difference
% time on nest incubating per nest	50.7±7.0 (27)(42-66)	49.3 ± 7.0 (27)(34-66)	n.s.
% time on nest brooding chick	52.8±9.1 (12)(46-67)	47.2±9.1 (33-54)	n.s.
Foraging trip duration during incubation (hours)	10.7 ± 1.9 (14) (5.8-12.2)	9.5 ± 2.9 (30) (4.7-12.5)	n.s.
Trip duration during brooding (hours)	5.0±2.0 (13)(1.2-7.2)	4.0±2.0 (7) (1.1-7.3)	n.s.
Foraging range during incubation (km)	50.2±30.8 (16) (22-111)	85.3±26.3 (19) (54-148)	**
Foraging range during brooding (km)	40.1±29.5 (10) (9.8-87.4)	30.5±327.0 (7) (20-114.4)	n.s.
% time in flight when at sea	69.3±13.1 (24)(50.9-94.8)	66.3±116.0 (32)(36.0-90.6)	n.s.
Number of landing / hour	35.7±12.1 (16)(12.7-64.1)	24.8±8.6 (14)(13.6-40.8)	*
Number of dives per hour	9.1±6.5 (5) (1.8-19.4)	2.8±1.5 (8) (0.6-4.8)	*
Maximum depths attained (m)	1.9 ± 0.2 (5)(1.6-2.4)	2.0 ± 0.11 (8)(1.4-2.2)	n.s.
Duration of plunge dives (sec)	1.62±0.17 (1-6)(334)	1.84±0.92 (1-8) (181)	*
Average diving depths of plunge dives (m)	0.93±0.47 (334)	1.05±0.51 (181)	n.s.
Instantaneous flight speed (overall foraging trip) km h^{-1}	34.1±15.8 (6307)	37.1±19.2 (8570)	n.s.
Travelling speed km h^{-1}	37.4±13.4 (5593)(10-95)	39.6±11.2 (7769)(10-84)	n.s.
Sinuosity	1.55±1.44 (4822)	1.45±1.4 (6545)¶	n.s.
% time spent flapping when travelling	29.9±10.5 (28) (9.0-51.1)	34.3±6.3 (15)(20.1-79.5)	n.s.

Table 3 Comparison of the diet of males and females (samples sizes in parentheses) according to the prey type (by numbers) and to the mass and size of prey captured.

a)

Class	Family	Male	Females
Squids	Ommastrephidae	54.3% (63)	48.0 % (71)
	Unidentified	4.3% (5)	6.8 % (10)
Fishes	Exocetidae	19.8% (23)	25% (37)
	Hemiramphidae	14.7% (17)	6.8 % (10)
	Carangidae	0 % (0)	1.3 % (2)
	Unidentified	6.9 % (8)	12.2 % (18)

b)

		Males	Females	Test
Ommastrephidae	Mass of prey (g)	9.7±5.7 (100)	9.9±6.6 (124)	$F_{1,222}$=0.03, p=0.85
	Body length (mm)	70.8±8.9 (100)	70.7±9.8 (124)	$F_{1,222}$=0.002, p=0.96
Exocetidae	Mass of prey (g)	62.7±21.8 (22)	69.9±25.1 (26)	$F_{1,46}$=1.14, p=0.29
	Body length (mm)	163.8±25.12 (22)	170.1±26.1 (26)	$F_{1,46}$=0.70, p=0.40
Hemiramphidae	Mass of prey (g)	28.8±7.8 (15)	31.3±4.7 (9)	$F_{1,22}$=0.76, p=0.39
	Body length (mm)	129.6±10.9 (15)	133.4±6.11 (9)	$F_{1,22}$=0.917, p=0.35

LEGENDS OF FIGURES

Figure 1 – Changes in the body condition of males and females red-footed boobies over the study period.

Figure 2 – Frequency distribution of flight speeds measured by GPS at 10 sec intervals in males and females.

Figure 3 – Three foraging trips of red-footed boobies fitted with GPS. Grey dots indicate active foraging (speeds lower than 10 km/h). Top: return trip of a female with foraging activity at the extremity; Middle: return trip of a male with multiple foraging throughout the trip: Bottom: looping track of a male.

Figure 4 – Frequency distribution of time spent at various distances from the colony (left) or at various % of maximum foraging range (right) by incubating (top) and brooding (bottom) males and females red-footed boobies.

Figure 5 - Foraging areas of red-footed boobies during incubation as shown by density contour plots from kernel estimates of the amount of time spent at sea, for females (left) and males (right) red-footed boobies. Range: dotted line, 95% density level, full line, core area 50% bold line.

Figure 6 –Frequency distribution of diving depths by males and females red-footed boobies during plunge-dives.

Figure 1

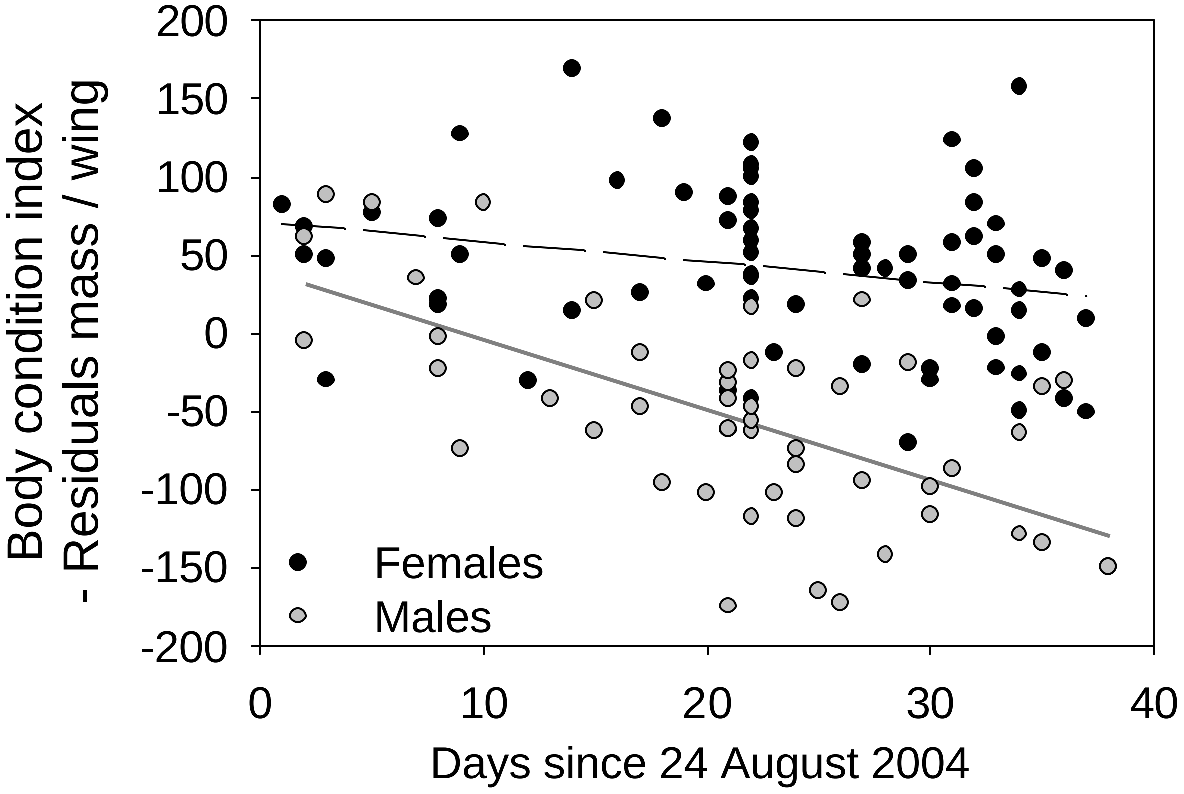

200
150
100
50
0
-50
-100
-150
-200
Body condition index
- Residuals mass / wing
● Females
○ Males
0
10
20
30
40
Days since 24 August 2004

Figure2

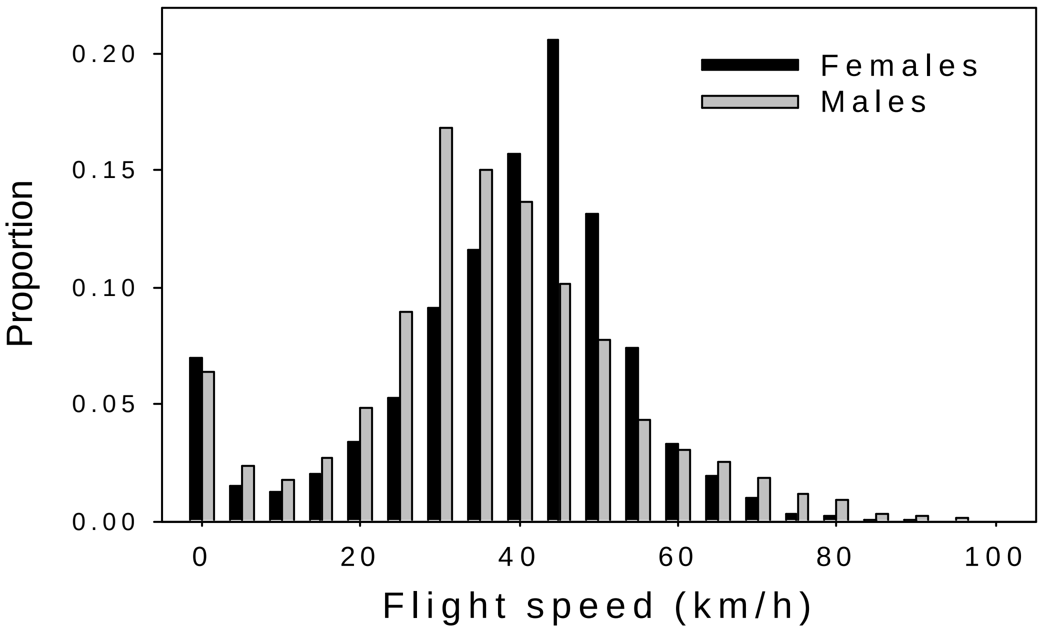

Females
Males
Proportion
0.20
0.15
0.10
0.05
0.00
0
20
40
60
80
100
Flight speed (km/h)

Figure 3

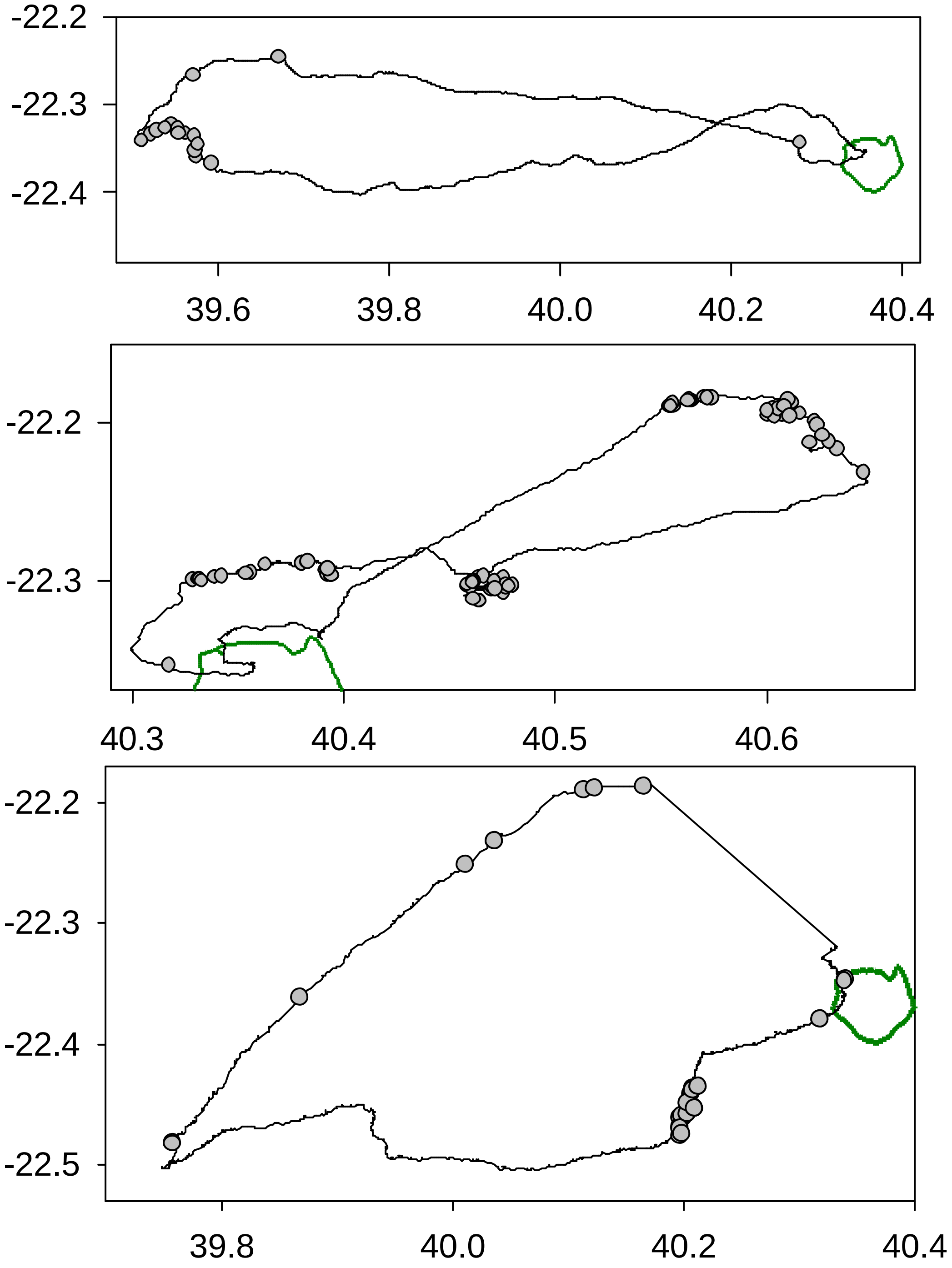

-22.2
-22.3
-22.4
39.6
39.8
40.0
40.2
40.4
-22.2
-22.3
40.3
40.4
40.5
40.6
-22.2
-22.3
-22.4
-22.5
39.8
40.0
40.2
40.4

Figure 4

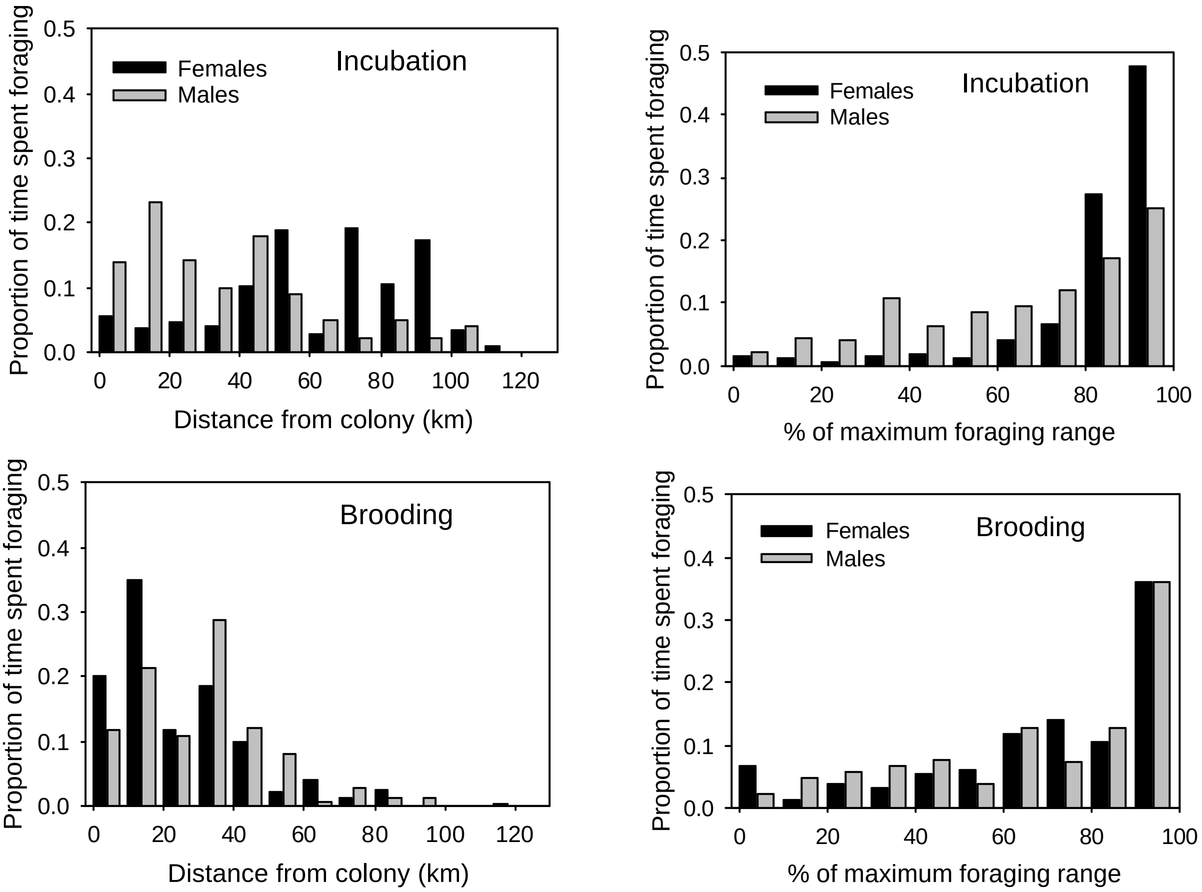

Incubation
Females
Males
Proportion of time spent foraging
0.0
0.1
0.2
0.3
0.4
0.5
0
20
40
60
80
100
120
Distance from colony (km)
Incubation
Females
Males
Proportion of time spent foraging
0.0
0.1
0.2
0.3
0.4
0.5
0
20
40
60
80
100
% of maximum foraging range
Brooding
Proportion of time spent foraging
0.0
0.1
0.2
0.3
0.4
0.5
0
20
40
60
80
100
120
Distance from colony (km)
Brooding
Females
Males
Proportion of time spent foraging
0.0
0.1
0.2
0.3
0.4
0.5
0
20
40
60
80
100
% of maximum foraging range

Figure 5

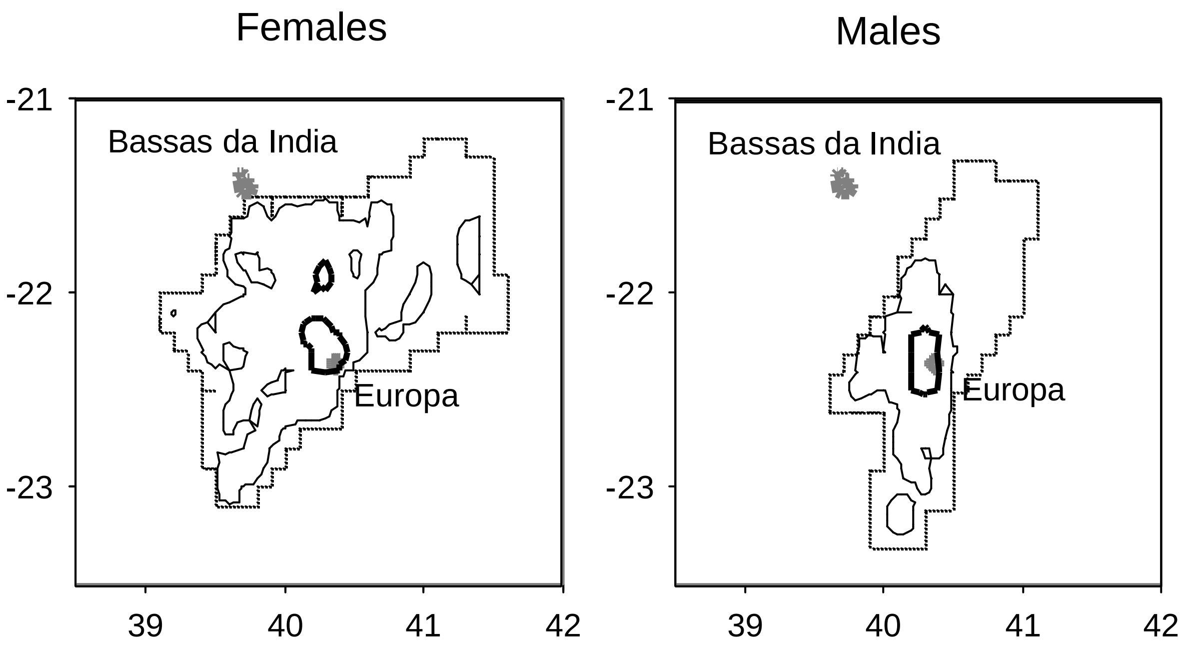
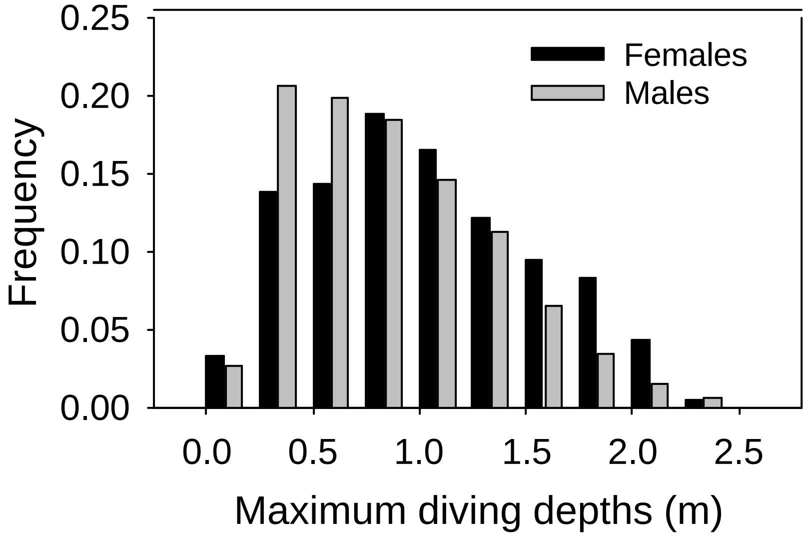


Figure 6


0.25
0.20
0.15
0.10
0.05
0.00
Frequency
Females
Males
0.0
0.5
1.0
1.5
2.0
2.5
Maximum diving depths (m)