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DIVING DEPTHS OF TWO TROPICAL PELECANIFORMES: THE RED-TAILED TROPICBIRD AND THE RED-FOOTED BOOBY[1]

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Abstract. The diving ability of two tropical Pelecaniformes, the Red-footed Booby (*Sula sula*) and the Red-tailed Tropicbird (*Phaethon rubricauda*) was studied on Europa Island, southern Mozambique Channel, using capillary depth recorders fitted on breeding adults. Both species mainly exploited the first 4 m of the water column. Although such a depth can be reached solely by passive plunge diving, the range of depths reached by the two species suggests that they may, at least sometimes, use their feet and wings to perform active underwater pursuit swimming. Intraspecific comparison of the depth reached by Red-tailed Tropicbirds also suggests that this species may change its diving behavior seasonally.

Key words: diving depth, feeding ecology, Red-tailed Tropicbird, Red-footed Booby, Phaethon rubricauda, Sula sula, *Europa Island.*

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Most boobies (tropical *Sulidae*) and all tropicbirds (*Phaethontidae*) are pelagic plunge diving seabirds (Ashmole 1971, Nelson 1978, Schreiber and Clapp 1987), foraging solitarily (tropicbirds, Masked Booby) or collectively (most boobies), and feeding mainly on flying fishes and squid (Ashmole and Ashmole 1967, Diamond 1974, 1975, Harrison et al. 1983). Plunge divers supposedly have limited diving capacities, the depth they reach depending mainly on the momentum gained during the plunge (Ashmole 1971). However, at least Cape Gannets (*Sula capensis*) can use their wings and feet to gain additional depth (Adams and Walter 1993). Here I report diving performances of two tropical plunge divers, the Red-tailed Tropicbird (*Phaethon rubricauda,* 0.8 kg) and the Red-footed Booby (*Sula sula,* 0.9 kg).

METHODS

The study was conducted on Europa Island (22°20′S, 40°22′E) in the southern Mozambique Channel. About 3,000 pairs of Red-footed Boobies and about 3,500

TABLE 1. Maximum diving depths (m) and gauge deployment durations (days) of Red-tailed Tropicbirds and Red-footed Boobies (mean ± SD) at Europa Island.

	Incubation	Chick-rearing	Both
Red-footed Booby			
depth	4.9 ± 2.0 (n = 22)	—	
duration of deployment	2.0 ± 0.6 (n = 22)	—	
Red-tailed Tropicbird			
depth	6.3 ± 2.0 (n = 36)	2.3 ± 1.0 (n = 28)	4.5 ± 3.0 (n = 64)
duration of deployment	5.0 ± 1.7 (n = 36)	1.2 ± 0.5 (n = 28)	3.3 ± 2.3 (n = 64)

All tests are t-tests. Interspecific comparisons of maximum diving depths: 1: All RTTB vs all RFB: $t_{84} = 0.17$, $P > 0.05$. 2: Incubating RTTB vs incubating RFB: $t_{56} = 3.45$, $P < 0.05$. 3: Chick-rearing RTTB vs incubating RFB: $t_{48} = 5.55$, $P < 0.001$. Intraspecific comparison of maximum diving depths: Incubating RTTB vs chick-rearing RTTB: $t_{62} = 9.6$, $P < 0.001$; Intraspecific comparison of duration of deployment: incubating RTTB vs chick-rearing RTTB: $t_{62} = 12.43$, $P < 0.001$.

pairs of Red-tailed Tropicbirds breed at Europa Island, together with six other seabird species (Barré and Servan 1988, Le Corre and Jouventin, in press). Field work was carried out from 28 November 1994 to 10 January 1995, on incubating Red-footed Boobies and incubating Red-tailed Tropicbirds, and in April 1996 on chick-rearing Red-tailed Tropicbirds.

I used maximum depth recorders (Burger and Wilson 1988), devices successfully used for studying diving depths of a variety of pursuit divers and plunge divers (see for instance Burger and Simpson 1986, Wilson and Wilson 1990, Chastel and Bried 1996). Maximum diving depth recorders consisted of 12-cm lengths of plastic capillary-tube (Tygon brand; internal diameter, 0.8 mm) lined with icing sugar and sealed at one end (Burger and Wilson 1988). Each tube (weight: 1 g, < 0.1% of bird body mass) was fitted on a central rectrice using waterproof adhesive tape. On recovered gauges, the length of tube still covered with icing sugar was measured to the nearest 0.5 mm. Maximum diving depth was calculated by the equation: $D = 10.08\ ([Ls/Ld]-1)$, where D is depth (m), 10.08 is the height (m) of a column of sea water equivalent to 1 atmosphere of pressure, Ls is the initial length (mm) of icing sugar and Ld the length (mm) of icing sugar after the foraging trip (Burger and Wilson 1988). The gauges were fitted on color marked adults. Incubating adults were checked once daily. During the chick-rearing period, 10 nests of Red-tailed Tropicbirds with a 60–80-day-old chick were observed continuously during 6 days from sunrise to sunset; all feedings were observed. Chick-rearing adults were handled just after delivering meals. Burger and Wilson (1988) identified various causes of error when using capillary tubes to study maximum diving depths. Condensation within the gauge tubes, caused by heating from the sun in a moist environment, could lead to overestimates of the maximum depths attained. This cause of overestimation may be important particularly in the tropics. To limit this cause of error, I removed the gauges which had condensation in the tubes after a foraging trip, retaining for analysis only those which had an unequivocal clear boundary between the dissolved and undissolved powder. Plunge diving and multiple immersions also can lead to an overestimation of depths attained. I used capillary tubes with small internal diameter (0.8 mm) and fitted them with the open side pointing toward the tail to limit this possible bias.

RESULTS

Twenty-two gauges, out of 27 deployed, were successfully recovered from Red-footed Boobies, and 64 from Red-tailed Tropicbirds (incubating adults: 36 out of 51 deployed, chick rearing adults: 28 out of 44 deployed). The mean maximum depths reached were 4.9 ± 2.0 m for Red-footed Boobies (range: 2.9–9.7 m) and 4.6 ± 2.7 m (range: 1–13 m) for Red-tailed Tropicbirds. There was no significant difference in diving performances between the two species when considering all the data together (Table 1). However, interspecific differences in diving depths appeared when considering incubating and chick-rearing Red-tailed Tropicbirds separately. Incubating Red-tailed Tropicbirds reached greater depths than incubating Red-footed Boobies in December 1994 (Table 1). On the other hand, incubating Red-footed Boobies dived to a greater depth than chick-rearing Red-tailed Tropicbirds (Table 1).

Intraspecific comparison showed that Red-tailed Tropicbirds dived to a greater depth when incubating than when rearing a chick (Table 1). However, the durations of foraging trips during the incubating and chick-rearing periods differed in the Red-tailed Tropicbirds of Europa Island, so that gauge deployment lasted almost five times longer in incubating birds than in chick-rearing birds (Table 1). Thus, there was a strong correlation between foraging trip durations and maximum diving depths when data on incubating and chick-rearing Red-tailed Tropicbirds were pooled together (Fig. 1). However, this relation was not significant when considering incubating and chick-rearing birds separately (Fig. 1). Although incubation shifts of Red-footed Boobies last from 1 to 4 days on Europa Island (Table 1), there was no correlation between duration of deployment and maximum depth recorded ($r^2 = 0.04$).

DISCUSSION

Plunge divers are supposed to exploit mainly the first few meters of the water column (Ashmole 1971). Indeed, 41% of the Red-footed Boobies studied reached a maximum depth of 2–4 m. These values are similar to those obtained by Adams and Walter (1993) on Cape Gannets, and are consistent with the hypothesis that boobies and gannets use the momentum gained during the plunge. However, the deepest depth record-

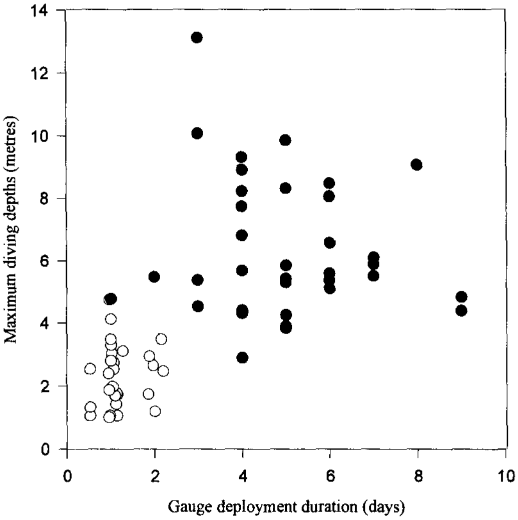

FIGURE 1. Relationship between gauge deployment durations (days) and the maximum depth recorded in incubating (black circles) and chick-rearing (open circles) Red-tailed Tropicbirds ($r^2 = 0.32$, $P < 0.001$ when plotting all the data together; $r^2 = 0.01$, $P > 0.05$ for incubating birds only, $r^2 = 0.04$, $P > 0.05$ for chick-rearing birds only).

ed (9.6 m) could hardly be reached solely by passive plunge diving, and this suggests that Red-footed Boobies can occasionally use their feet and/or wings to perform active underwater pursuit swimming, as found by Adams and Walter (1993) on Cape Gannets.

More than 90% of the chick-rearing Red-tailed Tropicbirds dived between 1 and 4 m, suggesting that during the chick-rearing period, this species performs mainly passive plunge diving to catch prey at or very close to the surface. Preliminary data on diet show that these prey (n = 282 prey items identified during the chick-rearing period) are squid (51.5%), dolphin-fishes (*Coryphoenidae,* 14.9%), and flying-fishes (*Exocetidae,* 14.5%). Remaining prey are needlefishes (*Belonidae*), juvenile tuna (*Scombridae*), and unidentified fishes.

During incubation, the depths recorded were much deeper (about 60% of the incubating Red-tailed Tropicbirds dived between 4 and 8 m), suggesting that this species may change its diving behavior seasonally. However, foraging trips were five times longer during incubation than during the chick-rearing period (Table 1). As mentioned in the Methods section, long duration of gauge deployment can lead to overestimation of the depth recorded (Burger and Wilson 1988).

Although I fitted the gauges in order to minimize this cause of error, the deeper depths found during incubation may in part be due to overestimation. However, there was no correlation between deployment durations of the gauges and diving depths recorded when considering incubation only, suggesting that my results are reliable. Thus, the difference in diving depths recorded during incubation and chick-rearing period may be related to changes in diving behavior of Red-tailed Tropicbirds. During incubation, the main prey items (n = 101 preys items identified) were squid (46.5%), flying-fishes (26.7%) and unidentified fishes (19.8%). There were very few dolphin-fish (0.9%). Although we lack data on the behavior of Red-tailed Tropicbird at sea, it is of interest to note that seasonal changes in diet is related to changes in diving depths recorded.

My data on the diving depths of Red-footed Boobies and Red-tailed Tropicbirds show that both species exploit mainly the first meters of the water column, performing mainly passive plunge diving. However, the range of depths recorded suggest that both species can occasionally (Red-footed Boobies) or seasonally (Red-tailed Tropicbirds) perform active pursuit swimming, depending upon the prey available to foraging birds.

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ABSENCE OF LOCOMOTOR-RESPIRATORY COUPLING DURING SIMULATED DESCENDING FLIGHT IN THE CACKLING CANADA GOOSE[1]

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Abstract. The locomotor and respiratory patterns of six cackling Canada Geese (*Branta canadensis minima*) were examined during simulated +10° descending flight to determine if locomotor-respiratory coupling occurred. In half the birds, there was no locomotor-respiratory coupling, the remainder exhibited minimal partial coupling. We hypothesize that the absence of locomotor-respiratory coupling is probably of little energetic significance as descending flights tend to be of short duration and reduced power output.

Key words: wind tunnel, locomotor-respiratory coupling, descending flight, Branta canadensis minima.

Locomotor-respiratory coupling occurs in birds during flight (Butler and Woakes 1980, Funk et al. 1993), and during quadrupedal and bipedal locomotion in mammals (Bramble and Carrier 1983, Young et al. 1992, van Alphen and Duffin 1994). Mammals usually complete one stride per respiratory cycle (1:1 frequency ratio), although humans exhibit a 2:1 frequency ratio (van Alphen and Duffin 1994). In birds, a variety of coupling ratios have been described, including 1:1 in pigeons (Butler et al. 1994), 3:1 in geese (Butler and Woakes 1980, Funk et al. 1993), and 5:1 in ducks (Berger and Hart 1970). In all cases where birds were engaged in sustained horizontal flapping flight, locomotor-respiratory coupling was exhibited almost continuously, with very few uncoupled cycles observed (Butler and Woakes 1980, Funk et al. 1993).

Locomotor-respiratory coupling may enable the mechanical assistance of ventilation by the locomotor muscles causing an overall decrease in the cost of locomotion (Berger et al. 1970). We hypothesized that if this is true, the reduced power output (Tucker 1968, Pennycuick 1989) and short duration of descending flight may minimize the significance of coupling (in terms of energetic savings) and result in an absence of locomotor-respiratory coupling. Thus, the purpose of the present investigation was to determine whether locomotion and respiration are coupled in cackling Canada Geese (*Branta canadensis minima*) during simulated descending flight.

METHODS

Twenty-one cackling Canada Goose eggs were collected under Canadian Wildlife Service permit NWT-S26 from Baffin Island and transported to the wind simulator facility in Pickering, Ontario, Canada. The eggs were incubated and candled daily to determine development. When pipped, the eggs were transferred to a brooder until hatching. Three eggs did not hatch and two goslings died three days post-hatching.

The 16 surviving geese were hand raised and imprinted on the wind simulator operator. As in Rothe et al. (1987), we found it advantageous to house the birds in the same room as the wind simulator so that they could grow accustomed to the noise. Furthermore, the home cages (152 × 213 × 182 cm) were located downwind of the flight cage so that the geese could become acclimatized to the wind. Geese were placed in the home cage 7–10 days prior to the appearance of the first flight feathers and fed proprietary poultry diet (Shur-Gain) supplemented with fresh grass and given water daily.

Geese were allowed into the flight cage six days a week for approximately 1 hr a day. The wind simulator operator was always present in the flight cage during flights, because this was found to enhance the birds' willingness to fly. Geese were exposed to varying wind speeds and encouraged to leave the cage floor by a variety of stimuli (stick waving, clapping, shouting, and lifting by hand). Air flow was adjusted to +10° early in the training period. The entire wind simulator

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