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The daily catch: Flight altitude and diving behavior of northern gannets feeding on Atlantic mackerel

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ABSTRACT

Predators utilize a variety of behavioral techniques to capture elusive prey. Behavioral flexibility is essential among generalist predators that pursue a diversity of prey types, and capture efficiency is expected to be intense during the breeding season for parents that engage in self- and offspring-provisioning. We studied the foraging behavior of parental northern gannets in the northwestern Atlantic (Gulf of St. Lawrence) when they were feeding on Atlantic mackerel almost exclusively. Data-loggers recorded short (mean duration: 6.3 s), high speed (inferred vertical speeds of up to 54.0 m^*s^{-1}, equivalent to 194 km^*h^{-1}), and shallow dives (mean depth: 4.2 m; maximum: 9.2 m). Dives tended to occur in bouts, varying between 0.3 and 4.6 per hour (mean = 1.6). During foraging, overall flight heights ranged from 0 to 70 m, with no clear preferences for height. Most plunge-dives were initiated at flight altitudes of 11–60 m (mean ± SE = 37.1 ± 2.8 m; range 3–105 m except for 1 of 162 dives that was initiated at the sea surface). Dive depth and flight altitude at plunge-dive initiation were positively and significantly correlated, though it appears that low flight altitudes were sufficient to reach dive depths at which mackerel were present. Almost all dives were V-shaped indicating that a high acceleration attack is the most effective strategy for gannets feeding on large rapid-swimming prey such as mackerel that owing to thermal preferences does not occur below the thermocline and are thus well available and essentially trapped in the water depths exploited by northern gannets.

1. Introduction

To maximize success and efficiency, predators use a variety of foraging and prey capture tactics (Hixon, 1982). Predation efficiency is particularly critical for parents provisioning themselves and their offspring (Orians and Pearson, 1979). Many seabirds adjust their aerial diving behavior and underwater pursuit of prey (Elliott et al., 2008a,b). Generalist predators with a broad diet breadth make flexible decisions about the most effective behavioral interactions with prey (Hamer et al., 2007; Harding et al., 2007; Paiva et al., 2010).

Red-footed boobies (*Sula sula*), for example, exhibit a series of very specific flight and aerial adjustments in their pursuit of tropical fishes (Weimerskirch et al., 2005). The closely-related northern gannet (*Morus bassanus*) also modifies its aerial and underwater diving behavior when pursuing different prey (Garthe et al., 2000). Ropert-Coudert et al. (2009a) demonstrated that the maximum dive depths reached using the plunge-diving technique was 10–11 m. Using a biomechanical model they show that little additional depth can be obtained from momentum alone when initiating a plunge from heights higher than 40 m. Comparisons of dive angles by Australasian gannets (*Morus serrator*) similarly showed that dive patterns were adjusted before the bird entered the water (Machovsky Capuska et al., in press), confirming that dive depth is determined in the aerial phase of the plunge as suggested by Ropert-Coudert et al. (2009a). Machovsky Capuska et al. (2011a) also showed that Australasian gannets altered the height of their foraging flights to the depth of fish schools showing that in these circumstances dive profile is associated with prey location, as suggested by Elliott et al. (2008a, 2008b).

Northern gannets feed on a diverse array of pelagic fishes and squid that range in weights from grams to hundreds of grams and that are returned to chicks in loads consisting of from tens of prey items to single large individual prey (Montevecchi, 2007). Of the prey that northern gannets consume and deliver to chicks, Atlantic mackerel (*Scomber scombrus*) have the highest lipid contents and energy density (Montevecchi et al., 1984). Atlantic mackerel is one of the largest and fastest swimming pelagic fish consumed by an aerial diving seabird weighing many hundreds of grams and exhibits maximum burst speeds of up to 5 m^*s^{-1} (He, 1993).

We had hypothesized previously that rapid short duration V-shaped dives were aimed at large pelagic fishes and squids and that extended deep U-shaped dives by gannets were directed towards schools of

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small pelagic fishes such as capelin (*Mallotus villosus*) and sandlance (*Ammodytes* spp.; Garthe et al., 2000). This was broadly confirmed for gannets feeding on a mix of pelagic fish prey during another study (Garthe et al., 2011).

Here we report on a study at the largest colony of northern gannets in the northwestern Atlantic in the Gulf of St. Lawrence, where gannets were almost exclusively feeding on Atlantic mackerel during the 2007 breeding period. We analyze the foraging behavior of central-place foraging northern gannets preying on Atlantic mackerel, through the application of different data-logging units. We focus on the following questions:

(1) How deep and long do gannets dive when preying primarily on Atlantic Mackerel?
(2) Does a distinct diel rhythm exist?
(3) How high do gannets fly when they search for prey, and from which altitudes do they initiate their plunge-dives?
(4) Is the flight altitude before the start of the plunge-dive related to the dive depth?
(5) How can the flying and diving behavior of northern gannets observed in this study be explained by the biology of the Atlantic mackerel as their main prey?

2. Material and methods

2.1. Study site

This study was carried out between 1 and 11 July 2007 on Bonaventure Island (48°29′ N, 64°09′ W), a 5 km^2 island located 3 km off the Gaspé Peninsula in the boreal waters of the Gulf of St. Lawrence, Québec, Canada. Bonaventure Island is the site of the largest gannet colony in North America (ca. 59,600 pairs in 2009, JFR unpubl. data).

2.2. Diet sampling

Dietary data were collected by approaching gannets at the periphery of the colony such that some birds regurgitated food loads, and from observations of food scraps and feedings in the colony. Furthermore, some birds regurgitated food while being handled for attachment or removal of GPS devices. Dietary data are presented as the percentage of total prey loads identified. For mixed prey regurgitations the respective proportions of the prey categories were calculated. In addition to samples collected during the above mentioned study period, archived data from the Canadian Wildlife Service were analyzed to provide a broader picture of food consumption by northern gannets on Bonaventure Island.

2.3. Capture and handling of birds

Adult gannets incubating eggs or having small chicks (max. 2 weeks old) were captured and recaptured after 1–7 days with a telescoping noose-pole. To minimize disturbance, nests were chosen on the periphery of the colony. To reduce any potential bias due to unexperienced birds breeding at the periphery of the colony, birds were selected from the third or fourth row from the outer edge. Parental behavior and egg and chick survival appeared unaffected at nests where we attached data loggers to one parent. Capturing took usually 2–3 min, and attaching devices and marking a bird lasted 5–10 min at maximum. All birds were cared for in accordance with the guidelines of the Canadian Council on Animal Care.

2.4. Data loggers used

Birds were equipped with either an altimeter or a GPS logger.

Altimeters (15 g, 65 mm length, 16 mm diameter) specifically designed for this study by earth & OCEAN Technologies (Kiel, Germany) consisted of a pressure and a temperature sensor. The range of the pressure sensor was set to include altitudes from 2000 m high through dives to ca. 7 m deep; measurements were taken at a 1 s interval. Dives deeper than ca. 7 m were also recorded but the value remained at the deepest available option (we checked the raw values of the pressure channel for this purpose). The resolution was ca. 2 m in air with an estimated accuracy of ca. 8.5 m, and 0.0024 m in water with an estimated accuracy of 0.1 m (information provided by earth & OCEAN Technologies). Data collected were further calibrated; see section on flight altitude analysis below. Nine birds were equipped with these loggers all of which were recaptured, with seven data sets obtained for data analysis.

GPS TD logs (100 × 48 × 24 mm, 70 g; earth & OCEAN Technologies, Kiel, Germany) were attached to six birds of which five were recaptured with downloadable data. GPS loggers were taped to body feathers on the lower back just above the uropygial gland with Tesa® tape (Garthe et al., 2011). Devices included temperature/pressure sensors and comprised about 2% of adult body mass. Only data on pressure (i.e. dive depth) were used for this manuscript.

2.5. Diving analysis

Dives were analyzed using MultiTrace-Dive (Jensen Software Systems) and were defined as immersions deeper than 0.3 m; shallower measurements were attributed to bathing and preening movements. Two different dive types can be distinguished in recordings from northern gannets (Garthe et al., 2000): i) V-shaped dives, being usually relatively short and shallow, and with the ascent period following almost immediately the descent period; ii) U-shaped dives, being relatively long and often deep, with time spent at depth between descent and ascent periods. Dives were analyzed differently for the two devices. As dive depth was limited to ca. 7 m (varying slightly between the specific devices according to the calibration protocols) in altimeters, dive depth analysis for greater depth was limited to GPS TD loggers. It is important to note however that all dives deeper than ca. 7 m were also recorded by the altimeters (see above). Time of day was analyzed by relating each dive to the next full hour (i.e. 05 = 04:30–05:29), following Davoren et al. (2010). Inter-dive times were analyzed per foraging trip and day separately, measuring the time from the offset of one dive to the onset of the next.

2.6. Flight altitude analysis

All pressure values from the altimeters were first corrected for changing air pressure values by incorporating hourly measurements at the nearby weather station in Gaspé (data were downloaded from the Environment Canada website: http://www.climate.weatheroffice.gc.ca/climateData/canada_e.html). This was achieved by adding/subtracting air pressure measurements from the pressure values provided by the altimeter sensor to standardise air pressure in the atmosphere (to e.g. 1000 hPa). Altimeters were attached atop tail feathers, so that they remained above water when birds were swimming in order to determine 0 m altitude. This pressure calibration of the data sets was carried out frequently based on the periods when the birds were swimming. Data from lower pressure values were turned into flying height values (a difference of 1 hPa equates to a difference of ca. 8.4 m altitude in air).

Flight altitudes were determined separately for travel flight segments (periods of continuous flight after leaving the colony area and before reaching the foraging area; not further analyzed in this manuscript) and foraging bouts (periods with dives that are spaced less than 20 min apart). Flight altitudes were classified into 10 m classes separately for each individual.

Vertical speeds in the air were derived from differences in altitude between successive measurements (that are available in 1 s intervals,