THE ROYAL SOCIETY biology letters

Development of flight performance in the brown booby

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Recd 14.10.03; *Accptd* 10.12.03; *Published online* 13.02.04

How do birds acquire flight skills after fledging? This issue is important, as it is closely related to variation in the duration of offspring care, the causes of which remain unknown. In this study, we raised hatchling brown boobies, *Sula leucogaster*, and attached an acceleration data logger to each bird at fledging to record its movements. This allowed us to quantify precisely the time spent flapping, gliding and resting. The duration of foraging trips and proportion of time spent gliding during flight increased with the number of days since fledging, whereas the proportion of time spent in flight decreased. This indicates that brown boobies gradually acquire efficient flight skills during the post-fledging period, which might be the proximate cause of the long post-fledging care period in this species. To the authors' knowledge, this is the first study to record precisely the ontogeny of flight behaviour in birds.

Keywords: development; flight; booby; acceleration; data logger

1. INTRODUCTION

Parents provide various forms of care to their young, including warmth, protection from predators, and food (Clutton-Brock 1991). To date, the reasons for variation in the duration of offspring care remain largely unknown. In birds, the factors that most affect the durations of incubation and nestling care are controversial (Lack 1968; Ricklefs 1993; Martin 1995). Even less is known about the duration of care once the young have fledged (i.e. are able to fly) or have left the nest (Nice 1943; Skutch 1976). One of the prevailing hypotheses is that the young acquire the skills of locomotion or foraging during this period (Ashmole & Tovar 1968; Fogden 1972; Higuchi & Momose 1981; Heinsohn 1991). To test this hypothesis, it is important to record precisely the behaviour after fledging. However, because young birds move freely after fledging, it is difficult to record their behaviour, and few studies have tested this hypothesis quantitatively, especially for large birds that have great locomotory ability.

Long-lived birds, especially Pelecaniformes or Charadriiformes, have a long period of post-fledging care, which can exceed 400 days in great frigatebirds, *Fregata minor*, and is *ca*. 180 days in black-naped terns, *Sterna sumatrana* (Schreiber & Burger 2002). During this period, young birds may acquire the skills of efficient locomotion and foraging (Hamer *et al.* 2002). Owing to the difficulty in observing behaviour during the post-fledging period, the development of locomotion and foraging performance in seabirds has not to our knowledge previously been examined (Hamer *et al.* 2002).

The brown booby (*Sula leucogaster*) lives in the tropics and has a long period of post-fledging care (Schreiber & Burger 2002). After fledging, young boobies make round-trips between the nest and the sea, and still beg for food when at the nest. In this study, hatchlings were hand-raised by observers. Acceleration data loggers were then attached to the young to record their behaviour after fledging (Yoda *et al.* 1999, 2001). Here, we discuss the development of flight performance in young brown boobies.

2. MATERIAL AND METHODS

This study was conducted on Nakanokamishima Island in the Yaeyama Islands (24°11′ N, 123°34′ E) from April to September 2001. The island hosts a breeding colony of *ca*. 500 brown boobies (Kohno & Ota 1991). Each brown booby hatches two chicks, and one of the chicks routinely kills its sibling within a few days of hatching (Nelson 1978; Drummond *et al.* 2003). We selected, from different nests, two second-hatched chicks that were in good condition. They were named A1 and A2, respectively. Their ages were estimated from culmen length, using growth curves for brown boobies on Nakanokamishima Island (H. Kohno, unpublished data). Their sexes were unknown. We raised and fed them, and they recognized us as parents. Body weight, wing length, culmen length, tail length and tarsus length were measured regularly.

When the young boobies started to practise flying on land, we attached a wire base to their lower back using glue. An acceleration data logger was attached to this base using cable ties. The data logger was easily removed by cutting the cable ties. The device, which weighed less than 3% of the mass of a booby, did not seem to disturb their behaviour. The acceleration data logger was a UWE-200D2G logger (12-bit resolution, 90 mm × 20 mm, 42.7 g; Little Leonardo, Tokyo, Japan), which records swimming depth and acceleration at 1 and 16 Hz, respectively (for details see Yoda *et al.* (2001)). The measuring range of this device is –4 to 4*g* ($g = 0.98\ \mathrm{m\ s^{-2}}$). The loggers recorded ventral-to-dorsal acceleration in the birds' movements. The depth resolution was 0.1 m.

Both boobies fledged at the age of 100 days. This is similar to what is found in nature (Nakanokamishima Island: H. Kohno, unpublished data; see also Nelson 1978). They made trips to the sea during the day, returned to the nest and begged at dusk, and slept in their nests during the night. We attached the data loggers in the early morning, and recovered them at night. Data were downloaded from the data loggers into a computer and analysed using IGOR PRO (v. 4.03, WaveMetrics, Inc., USA). We attached a dummy logger during the night that weighed the same as the real data logger. The dummy logger was then replaced with the real acceleration data logger the next morning. We fed the boobies with tropical fish when they begged.

The gravity acceleration component was removed using a high-pass filter (Ifdl v. 3.1, WaveMetrics, Inc., USA; Watanuki *et al.* (2003)). Videotapes of brown boobies in flight produced a constant signal at *ca*. 3.5 Hz. Therefore, we used a high-pass filter starting at *ca*. 2 Hz, which is well below the flapping frequency. When boobies were flapping continuously, the acceleration was clearly periodic (figure 1): the peak-trough or trough-peak duration corresponded to a single wing stroke (i.e. up to down or down to up). Take off and landing/diving at the beginning and end of each phase were clearly distinguished (see Ropert-Coudert *et al.* 2004) and all parts of flight session lacking periodical patterns were gliding (figure 1). The diving phase was distinguished by the depth records. The resting on the water surface was distinguished by changes in acceleration owing to sea waves (see Yoda *et al.* 2001); alternatively, the resting on land was readily distinguishable because little movement was recorded for a long time (see Yoda *et al.* 2001). For each trip, we calculated the duration of flapping, gliding and other activities (time spent resting and diving).

3. RESULTS

The trip duration (TD) increased with the number of days since fledging (*D*) for both birds (figure 2*a*; bird A1: $r^2 = 0.746$, $p < 0.001$, $\mathrm{TD} = 1.757 + 0.281D$; bird A2: $r^2 = 0.873$, $p < 0.001$, $\mathrm{TD} = 1.712 + 0.33D$).

DOI 10.1098/rsbl.2003.0157

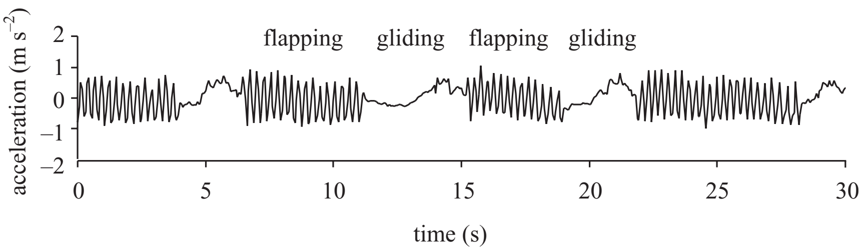

Figure 1. Measuring acceleration using a booby-borne data logger. The data logger sampled ventral-to-dorsal acceleration at 16 Hz. Clear alternations between flapping and gliding were observed.

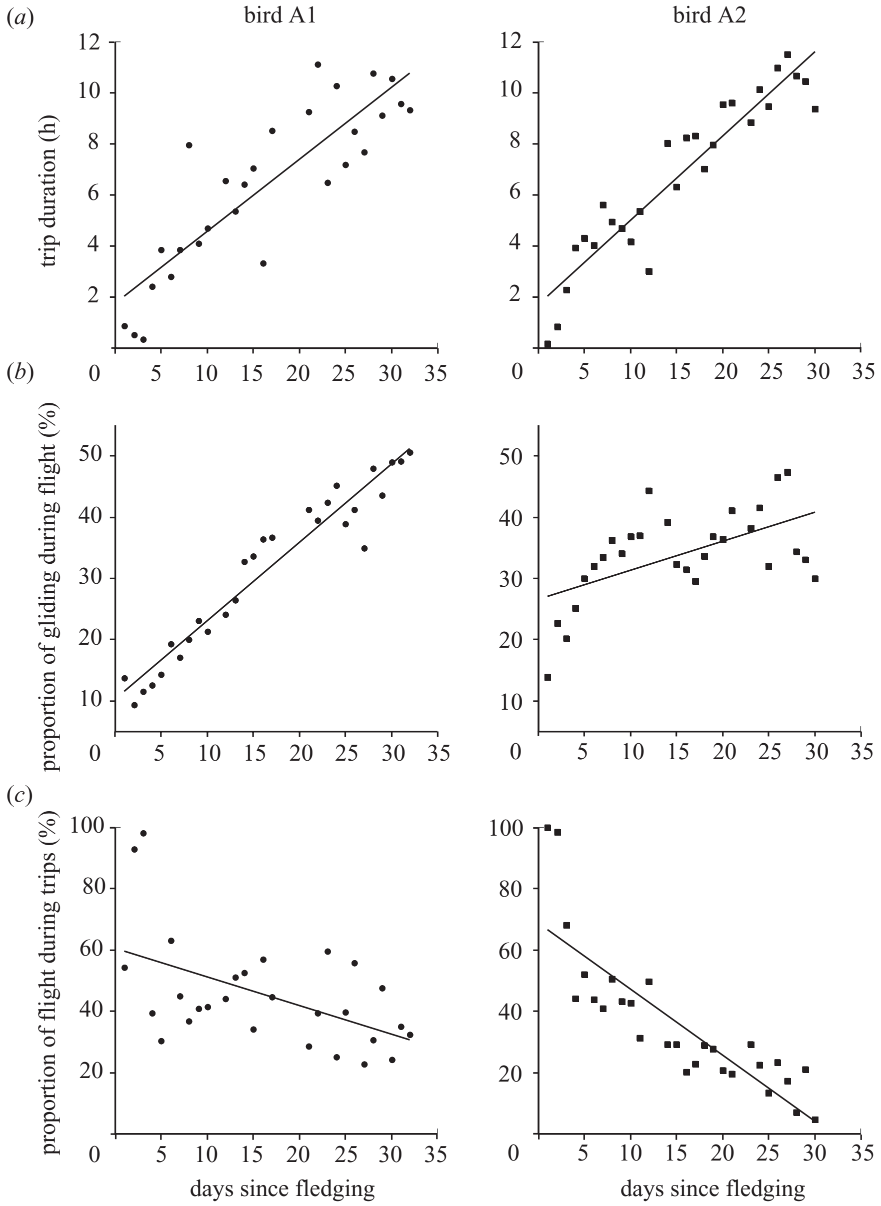

Figure 2. The relationship between the number of days since fledging (D) and (*a*) trip duration (TD), (*b*) proportion of time spent gliding during flight (PG), and (*c*) proportion of time spent in flight during trips (PF), for two boobies (birds A1 and A2). The equations describing the relationships in figure 2*a* are $\text{TD} = 1.757 + 0.281D$ ($r^2 = 0.746$, $p < 0.001$) and $\text{TD} = 1.712 + 0.33D$ ($r^2 = 0.873$, $p < 0.001$), in figure 2*b* are $\text{PG} = 10.374 + 1.276D$ ($r^2 = 0.932$, $p < 0.001$) and $\text{PG} = 26.667 + 0.473D$ ($r^2 = 0.328$, $p < 0.01$), and in figure 2*c* are $\text{PF} = 60.644 - 0.934D$ ($r^2 = 0.268$, $p < 0.01$) and $\text{PF} = 68.907 - 2.156D$ ($r^2 = 0.71$, $p < 0.001$), for birds A1 and A2, respectively.

The proportion of time spent gliding during flight (PG) increased with the number of days since fledging for both birds (figure 2*b*; bird A1: $r^2 = 0.932$, $p < 0.001$, $\text{PG} = 10.374 + 1.276D$; bird A2: $r^2 = 0.328$, $p < 0.01$, $\text{PG} = 26.667 + 0.473D$).

The proportion of time spent in flight during trips (PF) decreased with the number of days since fledging for both birds (figure 2*c*; bird A1: $r^2 = 0.268$, $p < 0.01$, PF $= 60.644 - 0.934D$; bird A2: $r^2 = 0.71$, $p < 0.001$, PF $= 68.907 - 2.156D$).

4. DISCUSSION

This is the first study, to our knowledge, to quantify the flight ontogeny of seabirds after fledging. We studied only two birds, but they showed similar trends. The pattern of development of physical parameters and the fledging period (both birds fledged at the age of 100 days) were also similar to those found in nature (Nakanokamishima Island: H. Kohno, unpublished data; see also Nelson 1978), which indicates that they matured naturally.

By the time that the boobies fledged, the growth of the culmen and wing length had already stopped, which is the same as in the wild (Nelson 1978). Therefore, a post-fledging period may not exist in terms of the development of physical parameters, although physiological changes (e.g. cardiovascular or respiratory changes) that are not apparent externally might occur. Alternatively, the post-fledging period might be important for the development of behaviour. How does the flight behaviour of boobies change?

The trip duration increased with the number of days since fledging (figure 2*a*). The boobies were able to travel for the whole day within 30 days of fledging. The proportion of time spent gliding during flight increased with the days since fledging (figure 2*b*). In terms of energy saving, gliding is more efficient than flapping during flight (Schmidt-Nielsen 1972; Rayner 1985). Shortly after fledging, the young brown boobies did not glide much, but they gradually made use of this ability, indicating that gliding may require more skill than flapping and that it takes young birds some time to acquire this skill.

The proportion of time spent in flight during trips decreased with the number of days since fledging (figure 2*c*), suggesting that the boobies were able to search and forage more efficiently as they developed. The acquisition of gliding skills may contribute to efficient trips to sea (figure 2*b*).

Brown boobies have a long duration of post-fledging care (Schreiber & Burger 2002). In this study, it took a long time for them to acquire efficient flight, which might be one of the proximate causes of the long post-fledging care period, as has been postulated (Ashmole & Tovar 1968; Fogden 1972; Higuchi & Momose 1981; Heinsohn 1991). Other factors also affect the duration of post-fledging care. For example, the latitude of breeding may be a factor, because tropical and Southern Hemisphere temperate species provide more extensive care than do Northern Hemisphere temperate species (Ricklefs 1969). To determine which factors most affect the duration of post-fledging care (Nice 1943; Skutch 1976), it will be necessary to record this behaviour precisely for several species.

In conclusion, during the post-fledging care period, young brown boobies gradually acquire gliding skills as they learn to search and forage more efficiently and to use the whole day for their trips. Young animals gradually acquire skills during the transition from dependence to independence.

Acknowledgements

The authors thank the Okinawa Regional Research Center, Tokai University, and its entire staff. They also thank K. Akata, A. Mizutani and T. Ohtani for their assistance in the field, and K. Sato and A. Kato for their help. This work was financially supported by grants from the Okinawa Regional Research Center, by a Grant for the Biodiversity Research of the 21st Century COE (A14) and by Research Fellowships from the Japan Society for the Promotion of Science for Young Scientists.

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