

## A new method to quantify prey acquisition in diving seabirds using wing stroke frequency

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### SUMMARY

To understand the foraging strategies of free-ranging diving animals, time series information on both foraging effort and foraging success is essential. Theory suggests that wing stroke frequency for aerial flight should be higher in heavier birds. Based on this premise, we developed a new methodology using animal-borne accelerometers to estimate fine-scale temporal changes in body mass of a pursuit-diving, piscivorous seabird, the European shag, *Phalacrocorax aristotelis*. We hypothesized that variations in body mass determined from changes in wing stroke frequency before and after a series of dives would be related to the amount of prey captured. The estimated net gain in body mass during a foraging trip was highly variable, ranging from -30 to 260 g, values that were extremely similar to food loads obtained from shags on the Isle of May in previous years using water-offloading and nest balances. Load sizes estimated using the wing stroke method were strongly and positively related to both cumulative flight time and return flight time. At the trip level, load size was unrelated to cumulative dive bout duration and the total amount of time spent underwater. However, highly significant relationships were apparent at the individual bout level, with birds showing bigger mass gains following longer dive bouts. Results from this study are therefore extremely encouraging and suggest that changes in body mass determined from changes in wing stroke frequency may provide a reliable method of obtaining short- to medium-term information on foraging effort and success of diving seabirds.

Key words: acceleration, data logger, flight, foraging, seabird, *Phalacrocorax aristotelis*.

### INTRODUCTION

Since the deployment of the first time-depth recorder on a Weddell seal (*Leptonychotes weddellii*) in 1963, animal-borne loggers have become increasingly sophisticated and it is now possible to investigate behaviour of a wide range of diving animals under natural conditions (Kooyman, 2004). Although devices can now provide detailed recordings of many behaviours, important details such as determining when a free-ranging individual encounters prey and the amount of prey consumed remain difficult to estimate. Various methods have been tried, including animal-borne cameras to record temporal and spatial patterns of prey encounter (Davis et al., 1999; Grémillet et al., 2006; Hooker et al., 2002; Mitani et al., 2004; Ponganis et al., 2000; Watanabe et al., 2003; Watanuki et al., 2007), acoustic loggers to identify prey encounters of echolocating cetaceans (Akamatsu et al., 2005; Miller et al., 2004a; Watwood et al., 2006) and loggers to measure beak opening (Plötz et al., 2001; Takahashi et al., 2004; Wilson, 2003; Wilson et al., 2002). To identify the precise timing of prey capture and mass of prey ingested, changes in oesophageal and stomach temperatures (Charrassin et al., 2001; Ropert-Coudert and Kato, 2006; Ropert-Coudert et al., 2001; Wilson et al., 1995) have been used, while nest balances have been employed to estimate the total amount of prey caught during a foraging trip (Grémillet et al., 1996). However, all these methods have some limitations and sources of error, thus hindering progress in understanding the foraging ecology of diving species, many of which are of major conservation or economic importance.

Alternative techniques for quantifying underwater foraging success are therefore being explored. One promising approach has developed from the observation that swimming movements of diving animals are strongly influenced by the total density of their bodies (Miller et al., 2004b; Nowacek et al., 2001; Sato et al., 2002; Sato et al., 2003; Skrovan et al., 1999; Watanabe et al., 2006; Williams et al., 2000). For example, time-depth profiles of deep-diving seals (grey seal, *Halichoerus grypus*, and northern elephant seal, *Mirounga angustirostris*), where the buoyancy of an individual is determined by the ratio of lighter lipid to heavier lean tissue, are characterized by a drift phase (Beck et al., 2000; Crocker et al., 1997; Webb et al., 1998). Biuw et al. monitored temporal changes in drift rates of newly weaned pups of southern elephant seals (*Mirounga leonina*) during their first foraging trips at sea (Biuw et al., 2003). All seals showed a similar trend: drift rates were initially positive but decreased over the first 30–50 days after departure. Over the following ~100 days, drift rates again increased gradually, while during the last ~20–45 days drift rates remained constant or decreased slightly. These temporal changes were considered to correspond to relative changes in foraging success over the course of the trip (Biuw et al., 2003).

Unfortunately, the drift rate method is not applicable to diving seabirds because total body density is mainly affected by the volume of air kept in the body (Lovvorn et al., 1991; Sato et al., 2002; Wilson et al., 1992). However, the approaches being developed for marine mammals did stimulate us to think about other indirect methods that might be appropriate for investigating

foraging success in marine birds. Many seabirds make foraging trips in which they fly between a series of locations at each of which they make a series of dives (a dive bout). During these flights, birds stroke their wings in order to provide lift. Within a species it is likely that wing size and shape are similar and thus heavier birds will need to stroke at a higher frequency than lighter individuals (Rayner, 1987). According to some comparative studies, body mass of many species of flying bird changes seasonally, and within a species wing stroke frequencies show corresponding fluctuations (Gudmundsson et al., 1995; Pennycuik, 1996). However, to our knowledge, no previous study has taken advantage of this relationship and attempted to use wing stroke frequency to estimate foraging success of individual seabirds.

Typically, video recording has been used to measure stroke frequency in flying birds (Pennycuik, 1990; Pennycuik, 1996). However, this method is unsuitable for longitudinal measurements of a single individual over prolonged periods such as during a foraging trip. Animal-borne video cameras can record flipper movements of marine mammals (Davis et al., 2001; Skrovan et al., 1999; Williams et al., 2000) and emperor penguins, *Aptenodytes forsteri* (van Dam et al., 2002), but the devices are too large to be deployed on free-ranging flying birds. Animal-borne accelerometers have previously enabled us to obtain dominant stroke frequencies for aerial flight during foraging periods of a range of species, including razorbill (*Alca torda*), common guillemot (*Uria aalge*), Brünnich's guillemot (*U. lomvia*), rhinoceros auklet (*Cerorhinca monocerata*), European shag (*Phalacrocorax aristotelis*), South Georgian shag (*P. georgianus*), black-browed albatross (*Diomedea melanophris*) and streaked shearwater (*Calonectris leucomelas*) (Sato et al., 2007). Accelerometers can be used to record not only the dominant stroke frequency for each individual but also modulation of the stroke frequency throughout a certain period. Wilson et al. used accelerometers on cormorants to estimate activity-specific metabolic rate that indicated that returning birds worked harder than those flying out from the colony (Wilson et al., 2006). The modulation of the wing stroke

frequency of a flying bird is expected to correspond to fluctuations in body mass during a foraging trip. Thus, animal-borne accelerometers have the potential to provide detailed information on the amount of prey caught by an individual during a dive bout.

The European shag [*Phalacrocorax aristotelis* (Linnaeus)] is a medium-sized seabird that flies with continuous wing stroking. At the breeding colony on the Isle of May, off the coast of southeast Scotland, UK, shags typically make 1–4 foraging trips per day during chick rearing (Wanless and Harris, 1992). They feed benthically on small fish such as lesser sandeel (*Ammodytes marinus*) and butterfish (*Pholis gunnellus*), and food for the brood is transported back to the colony in the parent's stomach (Wanless et al., 1991a; Wanless et al., 1993a; Wanless et al., 1993b; Watanuki et al., 2007). In an earlier study using VHF telemetry and water-offloading to determine the mass of food loads brought back to the colony, load size was shown to be extremely variable, ranging from 8 to 208 g with a mean load mass of 106 g (Wanless et al., 1993b). These foraging characteristics, plus the tameness and accessibility of birds on the Isle of May, thus made this an ideal study system in which to carry out a pilot study to investigate whether foraging success of a diving seabird can be estimated from stroking frequency during aerial flight.

## MATERIALS AND METHODS

### Field work

Field work was conducted on the Isle of May, Scotland (56°11' N, 02°33' W) during the 2003 and 2006 breeding seasons. Birds brooding small to medium-sized chicks (14 in 2003 and two in 2006) were captured on the nest using a crook, in the evening or early morning, and a data logger was attached to the central back feathers using two plastic cable ties and waterproof tape to a piece of plastic netting (3 cm×5 cm) glued among the feathers with a fast-setting glue in 2003 and only waterproof tape in 2006. Body mass (to the nearest 10 g) was measured at deployment and recapture using a balance. Handling time was less than 10 min and after release every bird returned to its nest immediately and

Table 1. Performance of each bird during data obtained for the period of one day

Bird ID*	Body mass (kg)		Estimated range during final flight	Foraging trip		Dive		Flight		Stroke frequency (Hz) during flight			
	Measured Initial	Measured Final		No	Max. gain (g)	Total no. of bout	No.	Longest duration (sec)	Total dominant	Range in cruising	Max. at take-off		
	03M1	1.73	1.76	**	2	60	210	51	12	24	259	5.875	5.875–6.219
03M2	1.84	1.82	**	2	190	250	102	10	14	914	5.656	5.500–6.000	6.906
03F2	1.52	1.54	**	3	100	260	91	12	25	1050	5.938	5.750–6.250	7.125
03F3	1.50	1.50	1.50	6	–30	120	141	8	17	978	5.719	5.656–5.938	6.875
03F4	1.55	1.60	1.62	3	110	220	117	10	16	1012	5.594	5.438–5.844	6.844
03M5	1.82	1.92	2.07	3	210	230	59	8	17	673	5.594	5.563–5.938	6.563
03M6	1.91	1.92	**	3	230	250	160	7	11	665	5.563	5.375–5.781	6.563
03M7	1.86	1.80	1.80	3	0	190	88	8	15	396	5.438	5.406–5.719	6.875
03F7	1.60	1.81	1.86	4	60	210	120	8	18	904	5.875	5.594–6.031	6.688
03F8	1.78	1.70	1.76	5	0	120	66	6	13	133	5.625	5.469–5.781	6.906
03M9	2.05	1.90	1.84	4	20	70	63	12	16	733	5.438	5.344–5.563	6.438
03F9	1.75	1.60	1.65	4	50	220	119	24	36	759	5.656	5.594–5.969	7.000
03M10	2.06	2.20	2.34	5	70	260	122	17	22	717	5.656	5.563–6.000	7.281
03F10	1.69	1.80	1.74	4	20	220	86	19	26	769	5.875	5.875–6.250	7.094
06F1	1.59	No data	**	4	40	110	60	8	16	746	5.281	5.219–5.438	6.500
06F2	1.59	No data	**	5	50	230	152	10	19	971	5.469	5.250–5.688	6.594

\*I.D. is composed of year, sex and no. of pair. For example, 03M1 is 2003, male and pair no. 1.

\*\*No data because data recording stopped before final flight.

voluntarily departed for a foraging trip in the morning. Instrumented birds were recaptured in the evening following completion of their final trips of the day, and the logger retrieved.

### Instruments and data analysis

Acceleration data loggers (M190L-D2GT; Little Leonardo Ltd, Tokyo, Japan) were used to obtain detailed information on foraging activity over a 24 h period (maximum 28.2 h because of memory capacity). Each logger was 15 mm in diameter, 53 mm in length, had a mass of 18 g in air and recorded depth (1 Hz), two-dimensional acceleration (64 Hz, respectively) and temperature (not used in this study). Although the mass of the data logger in air was only ~1% of adult body mass, it is possible that energy expenditure during a trip might still be increased. However, the mass of a load of fish typically brought back after a foraging trip is much higher (mean 106 g) (Wanless et al., 1993b). Since there was no evidence of any obvious disruption to attendance behaviour of the instrumented birds, we therefore assumed that the data collected would be representative of normal flight behaviour. Furthermore, the aim of our study was to investigate relative changes in wing stroke frequency in relation to foraging success.

Loggers were positioned so as to detect longitudinal and dorso-ventral accelerations. Values recorded by the accelerometers were converted into acceleration ( $\text{m s}^{-2}$ ) with linear regression equations. To obtain the calibration equations, values recorded by each logger at  $90^\circ$  and  $-90^\circ$  from the horizontal were regressed against the corresponding acceleration ( $9.8 \text{ m s}^{-2}$  and  $-9.8 \text{ m s}^{-2}$ , respectively). Loggers measured both dynamic acceleration (such as wing stroking activities) and static acceleration (such as gravity). Low-frequency components ( $<1.5 \text{ Hz}$ ) of the fluctuation in longitudinal acceleration, along the long axis of the body, were used to calculate the pitch angle of the animal (Sato et al., 2003).

The instrumented birds made between two and six foraging trips over their respective deployment periods (Table 1). Acceleration and depth data were used to categorize the birds' behaviour into time on land, in the air (aerial flight) and in a dive bout, including dive and surface time on the water. Dives were defined as bird movements to depths greater than 1 m. Pitch angles were used to discriminate time at the surface (angle nearly  $0^\circ$ ), on land (angle  $>30^\circ$ ) and in aerial flight. Aerial flight was further characterized by a stable inclination of the body angle ( $7\text{--}21^\circ$ ) and periodic fluctuations in dorso-ventral acceleration.

Trip duration was defined as the interval between departure from and arrival back on land. Most trips started with a period of flight but in a few cases a bird initially went onto the water. Dive bouts were defined as a single or series of dives separated from the next bout by a period in flight, with bout duration estimated from the

start of the first dive to the end of the last dive and including all surface intervals between dives.

Power spectral density (PSD) was calculated from entire acceleration, along the dorso-ventral axis, of each bird using a Fast Fourier Transformation with computer program package IGOR PRO (WaveMetrics, Inc., Lake Oswego, OR, USA). Sub-samples for each flying period were used to determine the dominant stroke cycle frequency for each period. The minimum length of flight needed to calculate PSD with 0.03125 Hz resolution of frequency (equal to 18 g resolution of body mass) was 1 min. To investigate modulation of the stroke frequency throughout flying periods and obtain the maximum frequency at taking-off, a spectrogram of the dorso-ventral acceleration was calculated with IGOR PRO. When calculating the spectrogram, the Gabor spectrogram was selected. Frequency resolution was 0.125 Hz and generated a spectrum every 64 points (1 s). Calculated linear amplitude was expressed by colour accordingly (Fig. 1A).

### Theoretical background

According to Rayner (Rayner, 1987), a simple argument for the scaling of flight power and speed was first given by von Helmholtz (von Helmholtz, 1874). In steady level flight, lift ( $L$ ) and weight ( $mg$ ) must be in equilibrium:

$$L = mg, \quad (1)$$

where  $m$  is body mass (kg) and  $g$  is gravity acceleration ( $=9.8 \text{ m s}^{-2}$ ). The lift is expressed by:

$$L = \frac{1}{2} \rho S C_L U^2, \quad (2)$$

where  $\rho$  is the density of the air ( $\text{kg m}^{-3}$ ),  $S$  is area of the wing ( $\text{m}^2$ ),  $C_L$  is the lift coefficient and  $U$  is speed of the wing section ( $\text{m s}^{-1}$ ). Substituting  $L$  in Eqn 1 by Eqn 2, we obtain the following relationship:

$$U \propto \sqrt{\frac{mg}{S}}, \quad (3)$$

which indicates that the wing speed  $U$  should be proportional to the square root of wing loading ( $mg/S$ ). Stroke cycle frequency  $F$  ( $\text{Hz}=\text{s}^{-1}$ ) is determined by the amplitude of stroking ( $A$ ) and the speed of the wing:  $F=U/2A$ . Thus, the stroke frequency is also expected to be proportional to the square root of wing loading as follows:

$$F \propto \frac{1}{A} \sqrt{\frac{mg}{S}}. \quad (4)$$

If the body mass ( $m$ ) alone varies, owing to feeding or consumption of fuel throughout foraging trips, while the wing

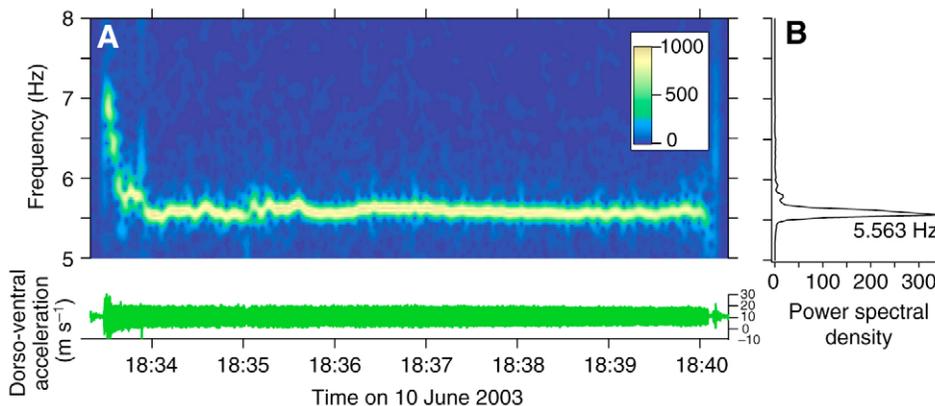


Fig. 1. (A) Spectrogram calculated from dorso-ventral acceleration (green line) of a shag (03F4) during an aerial flight for 403 s. (B) Power spectral density calculated during the flight indicates a clear peak at the frequency of 5.563 Hz.

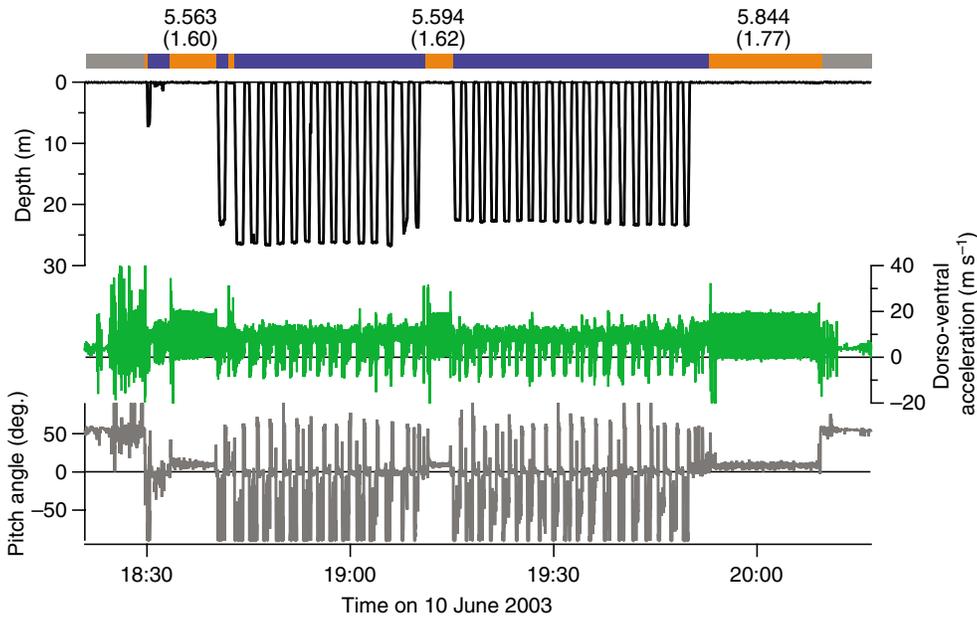


Fig. 2. An example of dives (black line), dorso-ventral acceleration (green line) and pitch angle (grey line) of a shag (03F4) during a foraging trip between two landings. Periods ashore in the colony, in flight and in dive bouts are indicated as grey, orange and blue bars at the top, respectively. Values on the orange bars are dominant stroke frequencies (Hz), and values in parentheses are estimated body masses (kg).

measurements ( $S$ ) and other variables ( $A$ ,  $\rho$ ,  $C_L$ ) remain unchanged, the expected relationship is  $F \propto m^{\frac{1}{2}}$ , as indicated by Pennycuik (Pennycuik, 1996). The wing stroking amplitude ( $A$ ) might increase with load. However, the stroking amplitude was not measured in the present study. Further work is needed to measure amplitude directly in shags. However, a payload experiment conducted on cockatiels (*Nymphicus hollandicus*) indicated that wing stroking amplitude was unaffected by the increase in loading (Hambly et al., 2004). Therefore, we assumed that  $A$  was constant and independent of any load carried.

If a bird, which was  $m_1$  (kg) and flew at stroke frequency  $F_1$  (Hz), changed its stroke frequency to  $F_2$  (kg), the mass  $m_2$  of the bird can be calculated by:

$$m_2 = \left(\frac{F_2}{F_1}\right)^2 m_1. \quad (5)$$

We measured body mass at deployment and recapture. The lighter mass was considered to be mass with empty stomach and was used as a bird-specific reference mass,  $m_1$ . Stroke frequency  $F_1$  at the departure flight was monitored by the accelerometer. The mass  $m_2$  of the birds flying at stroke frequency  $F_2$  can be calculated using Eqn 5.

### Statistics

For each bout, we examined the effect of dive bout duration and total underwater time on load size using Residual Maximum Likelihood Analysis (REML) (Patterson and Thompson, 1971) with individual as a random effect. For each trip, we analyzed the effect of cumulative duration of dive bouts, total underwater time, total flight duration and return flight time on load size during trips using REMLs with individual as random effect. We also analysed the effect of mass gain at sea and time on land on mass loss on land using REMLs with individual as a random effect.

### RESULTS

The acceleration data provided detailed information on stroke frequencies during aerial flights. Each bird had its own dominant stroke frequency, which varied from 5.281 Hz to 5.938 Hz

(Table 1). However, over the period of logger deployment, stroke frequencies of each individual showed clear temporal fluctuations. During a flight, a bird typically stroked at a higher frequency at take-off, after which stroke frequency equilibrated at a lower value throughout the subsequent cruising flight. A typical example is shown in Fig. 1, where the maximum frequency at take-off was 6.844 Hz and the dominant stroke frequency during cruising flight was stable at a lower value of 5.563 Hz. Dominant and take-off

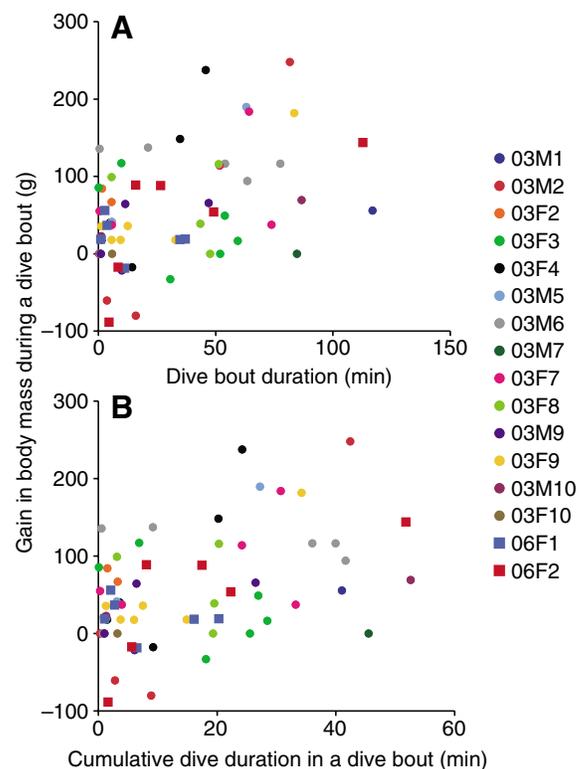


Fig. 3. Mass gain in each dive bout in relation to (A) dive duration and (B) cumulative dive duration. Symbols indicate study year (circles for 2003 and squares for 2006), and colours represent individuals.

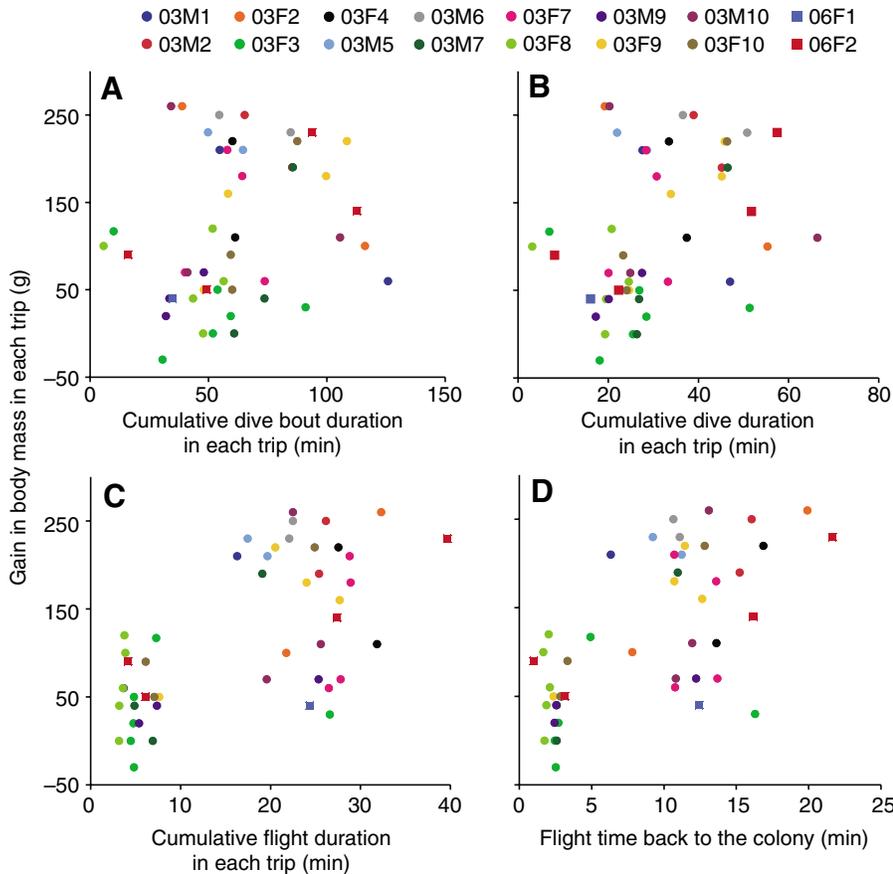


Fig. 4. Comparison of mass gain in trip with (A) cumulative dive bout duration, (B) cumulative dive duration, (C) cumulative flight duration and (D) flight time back to the colony in each trip. Symbols indicate study year (circles for 2003 and squares for 2006), and colours represent individuals.

bout level, load sizes were unrelated to cumulative dive bout duration (the sum of all dive bouts during the trip) (Fig. 4A) (REML:  $W=0.77$ ,  $P=0.38$ ) and total underwater time (Fig. 4B) (REML:  $W=3.40$ ,  $P=0.07$ ). There was a highly significant positive relationship between load size and both cumulative flight time (Fig. 4C) (REML:  $W=27.44$ ,  $P<0.001$ ) and return flight time (Fig. 4D) (REML:  $W=29.73$ ,  $P<0.001$ ). Thus, heavier loads were brought back to the colony after more distant foraging trips.

By comparing the wing stroke frequencies between return from one trip and departure on the next we could also estimate the net loss in body mass on land. Estimated decreases in mass varied from  $-17$  to  $250$  g and the amount of mass loss was independent of time on land, which varied between  $15.1$  and  $205.8$  min (Fig. 5A) (REML:  $W=0.00$ ,  $P=1.00$ ). However, mass loss ashore was positively related to net gain in the preceding foraging trip (Fig. 5B) (REML:  $W=64.75$ ,  $P<0.001$ ).

stroke frequencies for all available flights were determined using this method and showed that the dominant stroke frequency for each flight varied around the total dominant frequency for each bird (95–106% in Table 1).

Fig. 2 shows an example of a typical foraging trip composed of four dive bouts (blue bars) and five flights (orange bars). The bird first flew for 4 s and then made three shallow dives. The second flight lasted 403 s, after which the bird made one deep dive. A third flight lasting 39 s was followed by 14 deep dives, after which the bird flew for another 200 s and made another 19 deep dives. The flight back to the colony lasted 964 s. During the foraging trip, the dominant stroke frequencies increased from 5.563 Hz for the second flight, to 5.594 Hz for the fourth flight and 5.844 Hz for the fifth (Fig. 2). The first and the third flights in the trip were too short to allow estimation of the power spectral density. Estimated body masses corresponding to these stroke frequencies were 1.60 kg, 1.62 kg and 1.77 kg, respectively (Fig. 2). These changes suggest that the body mass of the bird increased by 20 g during the second and third dive bouts and by 150 g during the fourth dive bout.

Assuming that the main factor affecting these short-term changes in body mass was prey capture, we can thus use this approach to start to explore relationships between foraging success of European shags and other components of the foraging trip. When we analysed the effect of individual effort on load size at the bout level, we found strong positive relationships between load size and dive bout duration (Fig. 3A) (REML:  $W=15.22$ ,  $P<0.001$ ) and cumulative dive duration within a bout (Fig. 3B) (REML:  $W=15.46$ ,  $P<0.001$ ).

To investigate the total amount of prey caught during a foraging trip, we estimated the net gain in body mass by comparing stroke frequencies on the outward and inward flights. Values varied from  $-30$  to  $260$  g (Table 1). In contrast to the effect of efforts at the dive

## DISCUSSION

Results from this pilot study indicate that bird-borne accelerometers offer considerable potential as a means of quantifying fine-scale changes in body mass and thus determining the amount of prey captured by pursuit-diving seabirds. Although we could not directly calibrate the wing stroke method under controlled conditions, the range of food loads estimated here corresponded closely to two previous studies using water-offloading and nest balances, respectively (Wanless et al., 1998; Wanless et al., 1993b). As an additional check, where possible we compared the estimated body mass during the final flight back to the colony with the direct measurement of body mass on recapture (Table 1). In two cases, measured weights were 150 g less than those estimated using the wing stroke method, almost certainly because the birds had already fed their chicks before they were recaptured. Comparisons of the remaining values were all within a range of  $\pm 60$  g (Table 1), and this close correspondence further increases our confidence in the wing stroke technique.

The wing stroke method has several important advantages compared with other techniques. First, it is considerably less invasive than water-offloading or the deployment of internal devices such as stomach or oesophageal temperature loggers. Second, it can provide information at a finer temporal scale than either water-offloading or nest balances, where prey capture is integrated over the whole trip and success at the individual bout level cannot be investigated. Third, it is suitable for species such as shags that feed on relatively small prey items, such as lesser sandeels [mean mass of individual fish taken by shags was 3.2 g

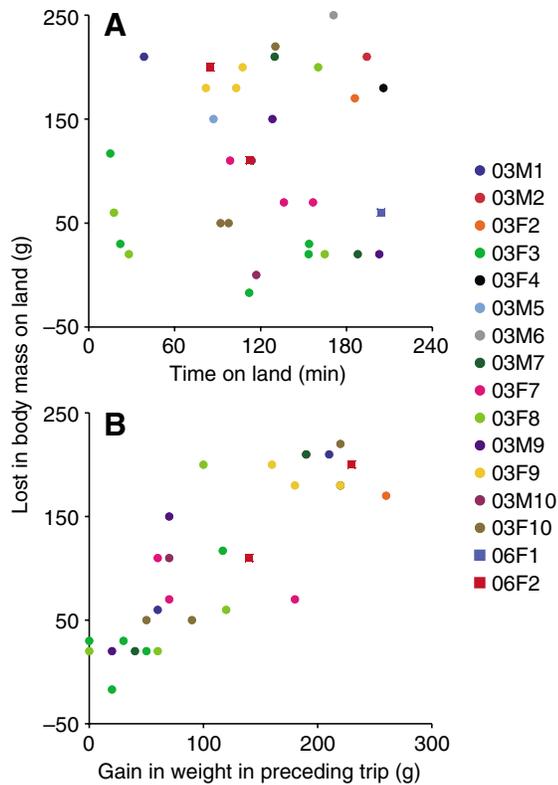


Fig. 5. Relationships of body mass lost on land to (A) time on land and (B) mass gain in preceding trip. Symbols indicate study year (circles for 2003 and squares for 2006), and colours represent individuals.

(Wanless et al., 1993b)], that are difficult to monitor using stomach temperature loggers, which perform best when large items are ingested.

However, the accelerometer wing-stroke method does have some limitations that must be kept in mind. First, memory capacity of the loggers currently limits data collection to ~24 h, making the technique unsuitable for pelagic, wide-ranging species. Second, the estimation of stroke frequency is only possible if a bird flies for more than 1 min. This interval is the minimum length needed to calculate PSD with a high resolution of frequency (0.03125 Hz) using a 64 Hz sampling interval. Most seabird species, even inshore feeders, fly for longer than this at the start and end of a trip so that the total amount of prey caught can be estimated in most cases. However, prey capture during dive bouts preceded or followed by flights shorter than this interval cannot be quantified. Third, changes in stroke frequency may not be only affected by changes in body mass. Wing stroking can potentially be affected by several other factors, for example a bird's flight behaviour (steady level flight and wing amplitude) and whether it is searching for prey or travelling, and the wind direction and speed relative to the bird's direction of flight. To evaluate the effect of body mass changes on stroke frequency, it is essential to do some further research, such as weight-dropping experiments, which have been conducted on sea turtles, *Caretta caretta* (Hays et al., 2004; Minamikawa et al., 2000), and Baikal seals (*Phoca sibirica*) (Watanabe et al., 2006). Finally, a key assumption underpinning the wing stroke method is that increases in a bird's body mass are primarily due to prey

being ingested. However, changes in body mass can also be due to feathers becoming waterlogged over the course of a dive bout.

This latter effect could be particularly problematic in species such as cormorants and shags that do not have a fully waterproof plumage. Ribak et al. demonstrated that, on average, water retention in the feathers of great cormorants (*Phalacrocorax carbo*) was 3% of body mass and the amount of water increased as a function of time in the water (Ribak et al., 2005). The positive relationship between mass gain and dive bout duration (Fig. 3A) might be caused by water trapped in plumage. However, mass gain in a trip was not related to cumulative dive bout duration in a trip (Fig. 4A), which contradicts the possibility that the gain in body mass was mainly caused by water in the plumage. Better plumage insulation has been suggested as a reason for lower energetic costs of diving in European shags compared with great cormorants (Enstipp et al., 2005) and, hence, amounts of water retained in the plumage are likely to be less in the former. Furthermore, European shags invariably flap their wings very vigorously before taking off from the sea, which is likely to get rid of some of the water trapped in the feathers at the end of the dive bout and more water may be expelled during take off. We are currently unable to partition changes in wing stroke frequency among these various contributing factors.

Although we assume that the main factor affecting these short term gains in body mass was prey capture, some amount of body mass may be lost due to defecation during dives (Wilson et al., 2004). Thus, our estimate of total amount of prey captured during a dive bout is likely to be conservative. According to a previous study (Wanless et al., 1997), in which masses of material defecated during a feeding trip were estimated by comparing food load for the trip estimated by stomach flushing and from nest balances, the mean mass of excreta was 7.2 g per trip. Thus, under the foraging regime typical of chick rearing at this study site, relatively little of the food was likely to have been lost as faeces by the time a parent returned to its nest.

The main aim of this study was to evaluate the wing stroke method as a means of estimating prey capture rates in diving seabirds. However, the trials also provided some useful insights into the foraging behaviour of shags during chick rearing. Previous work on the Isle of May found a highly significant positive correlation between load size and foraging range (Wanless et al., 1993b), and this relationship was also shown using the wing stroke method. The wing stroke method allowed us to develop this approach further and investigate prey ingestion during individual bouts. Shags on the Isle of May use a variety of foraging habitats (Wanless et al., 1991b), in some cases changing habitat within a trip (Watanuki et al., in press). We found a highly significant relationship between the amount of prey ingested and bout duration. Whilst we did not know precisely where birds were diving, further work that combined accelerometers with locational loggers, such as GPS, PTT or VHF radio tags, would enable us to build up a detailed picture of spatial variability in prey availability and start to determine foraging rules for this species.

It was clear that shags sometimes encountered very favourable feeding conditions during which they caught a large amount of prey in a short period. For example, female 03F2 caught 260 g of food in 17 dives during a bout lasting only 38.9 min and then returned to the colony. Many foraging trips lasted much longer than this (Fig. 4A,B), raising the question of why the female did not prolong her trip and increase her load still further. Part of the reason may be that the maximum stomach capacity of shags is around 220–250 g of food (S.W., personal observation) and thus the bird

would have had to stop feeding and digest some of the load. However, biomechanical constraints may also be important. According to theory, stroke frequency should be proportional to  $m^{-1/2}$  (Pennycuik, 1996; Rayner, 1987). Thus, as body mass increases, birds should increase wing stroke frequency in aerial flight. Shags stroked at very high frequencies when taking off (114–129% of the total dominant frequencies) (Table 1). However, these elevated levels did not last for more than 10 s and stroking frequency then equilibrated to lower values in cruising flight (Table 1, Fig. 1A). The dominant stroke frequencies associated with cruising flight varied around the total dominant frequency (95–106% in Table 1) for each bird. The observed range of sustainable stroke frequencies for an individual might therefore be within a range of economical frequencies for aerial flight. Thus, in the case of a bird encountering a good prey patch and having the option to prolong its dive bout to capture more prey items, if the increased load required an abnormally higher stroke frequency, this might be impossible to sustain to allow the bird to return to its nest. This may be a reason why they appeared to terminate their foraging trips prematurely when they encountered a good prey patch.

Although our main interest was in determining the amount of prey caught at sea, the difference in wing stroke frequency between the end of one trip and the start of the next provided an estimate of the decrease in body mass while the bird was in the colony. Mass losses occurred over a relatively short period, a pattern consistent with the decrease being primarily due to the bird feeding its brood rather than utilizing the prey for itself. Furthermore, mass loss was positively and significantly related to mass gained during the preceding trip, supporting the earlier suggestion that the bulk of the prey caught during a trip was fed to the young (Wanless et al., 1993b).

In conclusion, recently developed small accelerometers enabled us to monitor stroke frequencies of flying birds throughout their foraging trips, and a new method of analysis enabled us to relate changes in stroke frequency to changes in body mass. The technique would appear to have great potential for providing detailed information on foraging effort and success in a wide range of diving birds.

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