

RESEARCH ARTICLE

Poor flight performance in deep-diving cormorants

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SUMMARY

Aerial flight and breath-hold diving present conflicting morphological and physiological demands, and hence diving seabirds capable of flight are expected to face evolutionary trade-offs regarding locomotory performances. We tested whether Kerguelen shags *Phalacrocorax verrucosus*, which are remarkable divers, have poor flight capability using newly developed tags that recorded their flight air speed (the first direct measurement for wild birds) with propeller sensors, flight duration, GPS position and depth during foraging trips. Flight air speed (mean 12.7 ms⁻¹) was close to the speed that minimizes power requirement, rather than energy expenditure per distance, when existing aerodynamic models were applied. Flights were short (mean 92 s), with a mean summed duration of only 24 min day⁻¹. Shags sometimes stayed at the sea surface without diving between flights, even on the way back to the colony, and surface durations increased with the preceding flight durations; these observations suggest that shags rested after flights. Our results indicate that their flight performance is physiologically limited, presumably compromised by their great diving capability (max. depth 94 m, duration 306 s) through their morphological adaptations for diving, including large body mass (enabling a large oxygen store), small flight muscles (to allow for large leg muscles for underwater propulsion) and short wings (to decrease air volume in the feathers and hence buoyancy). The compromise between flight and diving, as well as the local bathymetry, shape the three-dimensional foraging range (<26 km horizontally, <94 m vertically) in this bottom-feeding cormorant.

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Key words: accelerometer, blue-eyed shag, data logger, flight speed, GPS tracking, power curve.

INTRODUCTION

Air and water have drastically different physical properties, and hence animals capable of moving in both media are expected to face evolutionary trade-offs regarding locomotory performances (Williams, 1999). Some seabirds (or waterbirds) are capable of both level flapping flight and prolonged diving, e.g. auks (Alcidae), cormorants (Phalacrocoracidae), boobies and gannets (Sulidae), loons (Gaviidae), grebes (Podicipedidae), ducks (Anatidae), shearwaters (especially the genus *Puffinus*) and diving petrels (*Pelecanoides*). The flight and diving performance of these birds might be compromised, because morphological and physiological demands are conflicting (Lovvorn and Jones, 1994; Wilson et al., 2008). For example, flapping flight favours smaller body sizes to allow for a larger margin of power available relative to the power required (Pennycuick, 2008). By contrast, breath-hold diving favours larger body sizes to allow for a larger margin of the oxygen stored relative to the oxygen consumed (Kooyman, 1989; Halsey et al., 2006). An extreme of the spectrum might be the Galápagos cormorant *Phalacrocorax harrisi*, which secondarily lost flight capability and has enhanced diving capability with the largest body mass among its family (Wilson et al., 2008). However, few studies have quantified both flight and diving performance of seabirds that dive and fly; consequently, empirical support for the possible compromise is sparse.

A major limitation in testing the prediction of evolutionary trade-offs is that, although the methods to record the diving behaviour of

seabirds (e.g. dive depth, duration and swim speed) using miniaturized animal-attached tags are now well established (Ropert-Coudert and Wilson, 2005), those to record flight behaviour (e.g. flight duration, distance and speed) are still immature. Recently, several methods to record flight duration were developed (Dall'Antonia et al., 2001; Tremblay et al., 2003; Pelletier et al., 2008; Sato et al., 2008), and support for the prediction was provided: when two species of auks were compared, the species that flew for longer durations dived shallower and for shorter durations than the other (Thaxter et al., 2010). Nevertheless, detailed behavioural and biomechanical analysis on the flight behaviour of seabirds in the context of the flight–diving compromise is still lacking. To do this, it is necessary to record more behavioural parameters during flight, such as GPS positions, which provide detailed horizontal paths (Weimerskirch et al., 2002).

Moreover, one of the most important parameters that directly affect flight energetics has never been continuously recorded for any bird: flight speed relative to air. The choice of air speeds by flying animals represents behavioural decisions depending on their ecological or physiological states (Norberg, 1981; Hedenstrom and Alerstam, 1995; Pennycuick, 2008; Grodzinski et al., 2009), and thus could provide useful information for the possible flight–diving compromise. For example, deep-diving seabirds might have only limited power available for flight compared with the power required, owing to their adaptations for diving. If so, they might choose the flight speed that

minimizes power requirement, rather than energy expenditure per distance (Pennycuick, 2008). This prediction can be tested by recording the flight air speed of seabirds in known ecological contexts (e.g. migrating, foraging and rearing chicks) and comparing it with the theoretical U-shape curve that represents the relationship between power requirement and flight air speed (Rayner, 1999). Previously, such studies collected the data of flight speed from ground-based remote observations (Welham, 1994; Pennycuick, 1987; Bruderer and Boldt, 2001; Pennycuick, 2001), where records are inevitably sporadic and limited to the birds flying closely to the observers. Therefore, recording flight air speed continuously with other behavioural parameters using animal-attached tags would be a promising approach to better understand the flight behaviour of birds.

In this study, we used newly developed tags to obtain detailed records of free-ranging flight behaviour as well as diving behaviour for a cormorant (here 'cormorant' is the general term for species in the family Phalacrocoracidae, whereas some of them are specifically called 'shags') (see Siegel-Causey, 1988). Parameters measured for flight behaviour included flight air speed (directly measured using the propeller sensor), GPS positions (which provide horizontal tracks and flight ground speed) and accelerations (which provide flight duration and wingbeat frequency). As a model of seabirds capable of level flapping flight and prolonged diving, we studied the Kerguelen shag *Phalacrocorax verrucosus* (Cabanis 1875), a member of the so-called blue-eyed shag complex (Siegel-Causey, 1988). Because of the remarkable diving capability in this complex (Quintana et al., 2007), we hypothesized that their flight performance is limited. Specifically, we would expect that: (1) the flight of shags is short, (2) resting behaviour is observed after flights, especially after long flights, and (3) actual flight air speed is close to the flight

air speed that minimizes the power requirement, rather than energy expenditure per distance. The first two predictions were examined using behavioural patterns (flight, diving and stay at the sea surface, monitored by accelerometers) overlaid on the GPS track during foraging trips. The last prediction was examined by comparing recorded flight air speed with the theoretical power curve, calculated for this species using existing aerodynamic models.

MATERIALS AND METHODS

Fieldwork and instruments

Fieldwork was conducted at Pointe Suzanne in the Kerguelen archipelago (49.43°S, 70.43°E) from December 2008 to February 2009, under a permit from the nature reserve and ethics committee of the Terres Australes et Antarctiques Françaises and Institut Polaire Français Paul Emile Victor. A total of 26 birds (20 males and 6 females) rearing one or two chicks were captured at the nests with a noose at the end of a 4 m fishing pole. They were then measured, weighed, equipped with data loggers (secured on the birds' backs using tape) and released. The birds were recaptured after one or two days, and the loggers were removed.

Several types of data loggers (Little Leonardo Corp., Tokyo, Japan) were used (Table 1): M190L-D2GT (15 mm diameter, 53 mm in length, 16 g in air) recorded depth, two-axis accelerations and temperature; W190L-PD2GT (21 mm diameter, 117 mm in length, 60 g in air) recorded swim or flight speed (see below), depth, two-axis accelerations and temperature; W1000-PD3GT (22 mm in diameter, 102 mm length, 90 g in air) recorded swim or flight speed, depth, three-axis accelerations and temperature; and GPL20 [49 mm in width and length, 21 mm in depth (with rounded corners), 61 g in air] recorded GPS positions. Sampling intervals were set at 1 s

Table 1. Descriptive information and foraging trips of Kerguelen shags

Individual	Sex	Body mass (kg)	Data logger	Data length (day)	Total duration at sea (h day ⁻¹)		Max. distance from colony (km)		
					Day 1	Day 2	Day 1		Day 2
							Trip 1	Trip 2	Trip 1
081223A	M	2.90	D2GT+e&O ^a	1	2.4				
081223B	M	2.75	D2GT+e&O ^a	1	8.2				
081224A	F	1.80	D2GT+e&O ^a	1	5.2				
081224B	F	1.80	D2GT+e&O ^a	1	7.8				
081226A	M	2.75	D2GT+e&O ^a	1	6.0				
081226B	M	2.30	PD3GT	1	4.5				
090101A	F	1.95	PD2GT	1	6.0				
090101B	F	1.95	PD3GT	2	8.6	3.7			
090105A	M	2.80	PD2GT	2	5.8	7.2			
090105B	M	2.50	PD3GT	2	5.0	8.4			
090106	M	2.60	D2GT+e&O ^a	1	13.2				
090110A	M	2.60	PD2GT	2	7.4	8.1			
090110B	M	2.25	PD3GT	2	5.9	4.8			
090110C	M	2.40	GPL	1	4.2		8.2		
090111	M	2.25	GPL+D2GT	1	5.3		4.9		6.7
090112A	F	1.85	PD2GT (air mode)	1	10.2				
090114A	M	2.50	PD2GT	2	9.3	5.9			
090114B	M	2.20	GPL+D2GT	2	4.3	6.2	6.7	2.4	7.2
090116A	M	2.15	PD2GT (air mode)	2	5.7	6.9			
090116B	M	2.30	GPL+D2GT	2	4.4	9.0	4.1	1.2	8.8
090118A	M	2.30	PD2GT (air mode)	2	4.4	3.9			
090118B	M	2.35	GPL+D2GT	2	7.6	10.8	22.4	10.9	26.2
090120A	M	2.50	PD2GT (air mode)	2	5.6	4.8			
090120B	M	2.35	GPL+D2GT	2	6.8	10.2	8.1		14.2
090122A	M	2.35	PD2GT (air mode)	2	7.0	8.0			
090122B	F	2.00	GPL+D2GT	2	3.0	3.2	1.3		1.4
Grand mean		2.31				6.5		8.1	

^ae&O represents the GPS logger from earth&OCEAN Technologies; data from this logger are not reported in this paper.

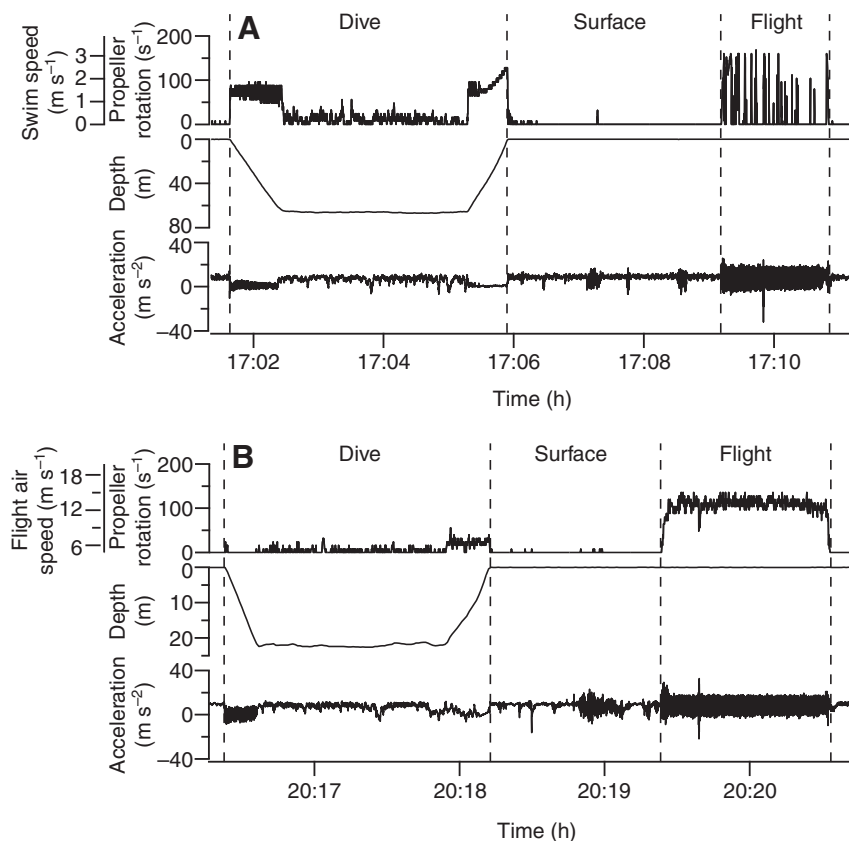


Fig. 1. Typical sequence of a dive, stay at the sea surface and flight of Kerguelen shags, shown by propeller rotation, depth and dorso-ventral acceleration. Propeller was set (A) in normal mode (bird ID: 090114A; 15 January 2009), where swim speed (but not flight speed) was recorded, and (B) in air mode (bird ID: 090120A; 20 January 2009), where flight speed (but not swim speed) was recorded.

for depth, temperature and GPS positions, 1/32 or 1/64 s for accelerations, and 1, 1/4 or 1/8 s for speed. All loggers had enough memories to record for the full deployment periods. GPS loggers [MiniGPSlog, 47 mm in length, 32 mm in width, 19 mm in depth (with rounded corners), 25 g in air; earth&OCEAN Technologies, Kiel, Germany] were deployed with the D2GT data loggers for some birds (Table 1); data from these loggers are not reported in this paper.

Data loggers in this study weighed 2.8% of the birds' body mass on average, which is relatively large and could potentially impact their flight and diving behaviour. Although we could not fully examine possible negative effects, the occasional regurgitations of the study birds during the data logger removal, and our unpublished observations with camera loggers (80 g), showed that the birds were successfully foraging. No birds equipped with data loggers abandoned their nests. Moreover, the relationship between dive depth and duration observed in this study (data not shown) closely resembled that reported previously with smaller data loggers (30 g) for the same species (Cook et al., 2008). Therefore, we assumed that the behaviour of study birds was not substantially altered, although further miniaturization of loggers is clearly needed in the future.

Flight air speed

The PD2GT and PD3GT data loggers have a propeller as the speed sensor. The shaft of the propeller has a magnet on the other side, so that the rotation of the propeller is detected as the magnetic signal. Normally, the propeller rotates well in the water when the animal is swimming, but not in the air when the animal is flying ('normal mode'; Fig. 1A). However, by adjusting the tightness of the nut on the propeller, it can be modified so that it works well in the air but not in the water (Fig. 1B). In this 'air mode', the propeller idles relative to the shaft (therefore the rotation value is not recorded) when speed is low, whereas it rotates with the shaft as in normal

mode when speed is high. Introducing the idle phase prompts the start of the propeller rotation, making it possible to record relative air speed during flight. The propeller loggers were set in normal mode for eight birds and in air mode for five birds (Table 1). In the case of one bird (ID: 090122B), air mode was accidentally switched to normal mode while the bird was at the nest (presumably by the pecks of the bird), resulting in air mode on the first day and normal mode on the second day.

Calibration experiments were made using the wind tunnels of Meisei University and Kogakuin University, Tokyo, Japan. The propeller loggers in air mode were set in front of the tunnel, and air speed was increased from 3 to 24 m s⁻¹ with an increment of 3 m s⁻¹. At 3 m s⁻¹, the propeller did not rotate continuously. At 24 m s⁻¹, it rotated continuously, but the rotation values recorded were very low, indicating that it idled relative to the shaft. At the medium range of 6–21 m s⁻¹, the propeller rotation was correctly recorded and stable within ± 3 rev s⁻¹ (± 0.2 m s⁻¹) around the mean value at each speed, except for infrequent instantaneous drops by ~ 20 rev s⁻¹ (1.5 m s⁻¹) at the speed of 21 m s⁻¹. At this range, the mean propeller rotation (Y , rev s⁻¹) increased with air speed (X , m s⁻¹) highly linearly as:

$$Y = 13.3X - 63.6 \quad (N=6, R^2 > 0.999). \quad (1)$$

Using this equation, the rotation value recorded during flight was converted into flight air speed.

Moreover, the effect of off-axis flow was examined with the tunnel at an air speed of 12 m s⁻¹ (close to the flight speed of shags; see Results) by setting the logger at an angle of 0 (head wind) to 90 deg (side wind) from the wind direction, with an increment of 10 deg. The propeller rotation decreased with the angle, and stopped at 80 and 90 deg. From 0–40 deg, the propeller rotation recorded at each angle agreed well (within 7 rev s⁻¹, or 0.5 m s⁻¹) with the value

predicted from the component of the air speed vector along the propeller logger axis [i.e. $12 \text{ m s}^{-1} \times \cos(\text{angle})$] and Eqn 1. This indicates that, if birds experience off-axis flow during forward flight, the propeller logger records the component of the total flow vector along the flying direction.

Wing morphology

Estimating the flight power curve of birds (see below) requires morphological information, including wingspan (i.e. distance from one wing tip to the other, with wings at full stretch) and wing area (i.e. area of both wings including the part of the body between the wings, projected on a flat surface). Therefore, in addition to the behavioural study, we captured 24 shags (12 males and 12 females) and traced their wings on a paper, before releasing them. A digital picture of the wing trace was taken with a reference square of known area, and the pixels of the wing trace and of the square were counted using IGOR Pro (WaveMetrics Inc., Lake Oswego, OR, USA) to calculate wing area. The mean values were used to estimate the flight power curve of Kerguelen shags (Table 2). Aspect ratio (dimensionless) was calculated as wingspan (m) squared divided by wing area (m²). Wing loading (N m⁻²) was calculated as body weight [i.e. body mass (kg) × *g* (9.8 m s⁻²)] divided by wing area (m²).

Flight power curve

To interpret the measured flight air speed, the theoretical U-shaped curve that represents relationship between the mechanical power requirement and flight speed is useful (Tobalske, 2007; Pennycuik, 2008). It indicates the two characteristic speeds: minimum power speed (V_{mp} , the speed at which the power requirement is minimum) and the maximum range speed (V_{mr} , the speed at which the distance flown with a given energy is maximum). V_{mr} is equivalent to the speed that minimizes energy expenditure per distance travelled. The Pennycuik and Norberg models (Pennycuik, 2008; Norberg, 1990) are widely used to estimate the power curve, with different assumptions for the profile power (see below). Because any existing aerodynamic models have uncertainties that can cause biased results (Rayner, 1999), we used both models and compared the results.

In both models, the total mechanical power for flight (P , W) can be expressed as:

$$P = P_{ind} + P_{par} + P_{pro}, \quad (2)$$

where P_{ind} is the induced power (i.e. the power needed to impart downward momentum of the air at a sufficient rate to support body weight), P_{par} is the parasite power (i.e. the power needed to overcome the drag of the body, excluding the wings) and P_{pro} is the profile power (i.e. the power needed to overcome the drag of the wings). P_{ind} is calculated as:

$$P_{ind} = 2km^2g^2 / V\pi B^2\rho, \quad (3)$$

where k is the induced power factor (dimensionless), m is the body mass (kg), g is the acceleration due to gravity (9.8 m s⁻²), V is the

flight air speed (m s⁻¹), B is the wingspan (m) and ρ is the air density (kg m⁻³). P_{par} is calculated as:

$$P_{par} = 0.5\rho S_b C_d V^3, \quad (4)$$

where S_b is the frontal area of the body (m²) and C_d is the drag coefficient based on frontal area (dimensionless). In the Pennycuik model (Pennycuik, 2008), P_{pro} is assumed to be independent of V for the range of V that birds normally use, for the following reason. P_{pro} depends on the airflow over the wings, which can be divided into two components: the airflow due to the forward movements of the bird and that due to flapping motion. Although the first component increases with V , the second component decreases with V due to decreased flapping frequency and amplitude, resulting in the total airflow that is approximately independent of V . P_{pro} in the Pennycuik model (Pennycuik, 2008) is calculated as:

$$P_{pro} = (4km^2g^2 / 3\pi B^2\rho^2 S_b C_d)^{1/4} C_{pro} S_w / B^2, \quad (5)$$

where C_{pro} is the profile power coefficient (dimensionless) and S_w is the wing area (m²). In the Norberg model (Norberg, 1990), P_{pro} is assumed to depend on V , and is calculated as:

$$P_{pro} = 0.5\rho S_w C'_{pro} V^3, \quad (6)$$

where C'_{pro} is the profile power coefficient for this model (dimensionless). P was then converted into the total metabolic power of the bird (M , W) as:

$$M = R(P / \epsilon + M_B), \quad (7)$$

where R is the respiration factor (dimensionless), ϵ is the efficiency to convert the mechanical power for flight into the metabolic power for flight (dimensionless) and M_B is the basal metabolic rate (W) (Pennycuik, 2008). M_B was estimated using the allometric equation specific to seabirds (Ellis and Gabrielsen, 2002):

$$M_B = 5.43m^{0.72}. \quad (8)$$

For each model, V_{mp} and V_{mr} were calculated as the V that minimizes M and M/V (which represents metabolic energy expenditure per distance travelled), respectively. In fact, converting P into M is not necessary to obtain V_{mp} , because P and M are minimized at the same V , as long as R , ϵ and M_B are independent of V (see Eqn 7). The parameters were set as follows: $k=1.2$ (Pennycuik, 2008), $m=2.4$ (the measured body mass + the mass of the propeller logger), $B=1.18$ (measured), $\rho=1.26$, $S_b=0.0149$ (the frontal area of birds calculated from girth measurements + the frontal area of the propeller logger), $S_w=0.18$ (measured), $C_{pro}=8.4$ (Pennycuik, 2008), $C'_{pro}=0.02$ (Rayner, 1979), $R=1.1$ (Pennycuik, 2008) and $\epsilon=0.23$ (Pennycuik, 2008). C_d is among the most influential parameters and is notoriously difficult to measure (Hedenstrom and Liechti, 2001; Pennycuik, 2008). We used the C_d value measured from captive cormorants gliding in the water (0.28) (Ribak et al., 2005). Our application of C_d measured in water to flight in air is justified by the fact that the Reynolds numbers of the shag's body were similar between flight (5.4×10^5) and swimming (6.4×10^5) in this study. In other words, flight and swimming were dynamically similar (Alexander, 2003) with respect to the flow pattern around the body, despite the difference in media.

An underlying assumption of these aerodynamic models is that birds are in level steady flight, without changes in potential or kinetic energy. Visual observations suggest that this assumption is generally met (see supplementary material Movie 1); however, shags do sometimes descend or ascend during flight. We therefore examined the sensitivity of V_{mp} and V_{mr} to the change of flight angle. In descending and ascending flight, the total mechanical power (P' ,

Table 2. Wing morphology of Kerguelen shags

	Male (N=12)	Female (N=12)	P^A
Body mass (kg)	2.5±0.2	2.2±0.1	<0.001
Wing span (m)	1.21±0.04	1.15±0.03	<0.0001
Wing area (m ²)	0.19±0.01	0.17±0.01	<0.0005
Aspect ratio	7.7±0.4	7.6±0.3	0.61
Wing loading (N m ⁻²)	127±12	126±10	0.81

Data are means ± s.d.

^A *t*-test was used.

W) could be estimated by adding the rate of change in potential energy (P_{PE} , W) to the right side of the Eqn 2 (Berg and Biewener, 2008) as:

$$P' = P_{ind} + P_{par} + P_{pro} + P_{PE}. \quad (9)$$

P_{PE} can be expressed as:

$$P_{PE} = mgV\sin\theta, \quad (10)$$

where θ is the flight angle relative to the horizontal (deg), with positive values indicating ascent and negative descent. Replacing P in Eqn 7 with P' allowed us to estimate V_{mp} and V_{mr} in ascending and descending flight. For example, by changing θ from 0 (level flight) to 5 deg (slightly ascending flight), V_{mp} decreased by 3.8 and 2.6 m s^{-1} in the Pennycuick and Norberg models (Pennycuick, 2008; Norberg, 1990), respectively. By changing θ from 0 (level flight) to -5 deg (slightly descending flight), V_{mp} increased by 5.4 and 3.4 m s^{-1} in the Pennycuick and Norberg models (Pennycuick, 2008; Norberg, 1990), respectively. These calculations show that the estimate for V_{mp} is indeed sensitive to the change of flight angle. By contrast, V_{mr} was not affected by θ in either model. (This can be explained mathematically. Equating the first derivative of M/V with respect to V to zero gives V_{mr} . The term θ is eliminated during the process.) In this study, the estimated V_{mp} and V_{mr} , assuming level steady flight, were compared only with the mean flight air speed of relatively long flights (>30s), where the effect of unsteady flight condition (takeoff, landing and possible occasional descent or ascent in the middle of flight) is expected to be small.

Behavioural data analysis

We used IGOR Pro with the package Ethographer (Sakamoto et al., 2009) to analyse the behavioural data. On the basis of acceleration and depth data, behaviour was categorized into diving, flight, stay at the sea surface and stay on land. Diving was defined as periods with depth >1 m, and flight was detected by high-frequency and high-amplitude fluctuation of dorso-ventral acceleration (Fig. 1). To distinguish between stay at the sea surface and stay on land, we used pitch angle, which is close to horizontal at the sea surface and upright on land. Pitch angle was calculated from low-frequency signals of longitudinal acceleration, and the values recorded just before the release of the birds was corrected to the horizontal level, because we kept the birds horizontally for ~10s before releasing. The dominant wingbeat frequency during flights was calculated for each individual, as the peak frequency in the power spectral density analysis of the dorso-ventral accelerations (Sato et al., 2007). The propeller rotation values recorded during swimming were converted into actual swim speed (m s^{-1}), based on an *in situ* calibration method using depth change and pitch angle (Sato et al., 2003). GPS positions were converted into UTM coordinates using Ethographer, allowing us to calculate the distance between the positions (and hence flight ground speed), accounting for the fact that the Earth's surface is not flat. As for mean air speed, the mean ground speed was calculated only for relatively long flights (>30s), so that the effect of unsteady flight condition could be minimized.

To test the relationships between the behavioural parameters, we used generalized linear mixed models (GLMM) with individuals as a random effect, using the software R and the package lme4 (The R Project for Statistical Computing, <http://www.r-project.org/>). The most parsimonious model was selected on the basis of Akaike's information criterion, and a chi-square test was used to determine the effect of term in the selected model. Statistical significance was set at $P < 0.05$. Means (\pm s.d.) are reported.

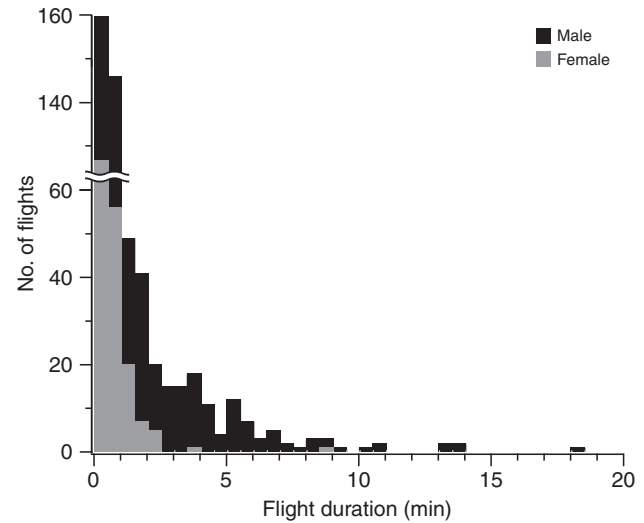


Fig. 2. Frequency distribution of flight duration for male (16 birds pooled) and female (nine birds pooled) Kerguelen shags.

RESULTS

All instrumented birds made foraging trips every day, and parameters for flights and diving were recorded (Tables 1, 3 and 4). Acceleration records from 25 birds showed that flights were short, with a grand mean of 104s (max. 1098s) for males and 51s (max. 534s) for females. Males flew for significantly longer durations than females (GLMM, $\chi^2=5.2$, $P < 0.05$, $N=741$). The frequency distribution of flight duration had a peak at 0–30s with a long tail for both males and females (Fig. 2). Flight air speed was recorded for a total of 61 flights (>30s) for five birds (grand mean 12.7 m s^{-1} ; Table 3, Fig. 3), excluding some flights where the propeller stopped temporarily. Flight ground speed was recorded for a total of 160 flights (>30s) for six birds (grand mean 13.0 m s^{-1} ; Table 3). The mean value was similar between air and ground speed, but ground speed was much more variable than air speed, as shown by a higher standard deviation. Diving behaviour was recorded for 25 birds, with a grand mean dive depth of 27.7 m (max. 94.2 m) for males and 10.4 m (max. 26.0 m) for females, and

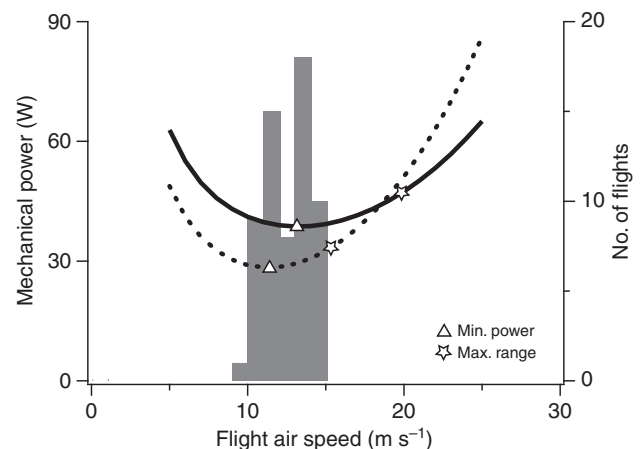


Fig. 3. Mechanical power curve for the flapping flight of Kerguelen shags, based on the Pennycuick model (solid line) and the Norberg model (dotted line) (Pennycuick, 2008; Norberg, 1990). Minimum power speed (triangles) and maximum range speed (stars) are shown for each model. Grey bars behind the curves represent the frequency distribution of air speed during flights (>30s) measured by propeller loggers (five birds pooled).

Table 3. Flight behaviour of Kerguelen shags

Individual	Flight duration (s)		Air speed (m s ⁻¹)	Ground speed (m s ⁻¹)	Wingbeat frequency (Hz)	Total flight duration (s day ⁻¹)	
	Mean	Max.				Day 1	Day 2
081223A	126±165	511 (8)			6.1	1005	
081223B	169±136	372 (12)			5.6	2025	
081224A	52±31	111 (16)			6.3	834	
081224B	48±40	131 (15)			5.6	721	
081226A	100±77	311 (19)			5.7	1900	
081226B	63±57	229 (18)			6.0	1131	
090101A	91±122	534 (15)			5.9	1367	
090101B	19±16	105 (104)			6.0	1489	507
090105A	266±282	1098 (18)			5.8	2553	2230
090105B	104±114	383 (31)			5.8	2105	1123
090106	61±80	310 (16)			5.8	977	
090110A	167±151	608 (28)			6.2	2313	2365
090110B	78±55	190 (10)			6.2	386	396
090110C							
090111	31±22	112 (23)		12.8±5.6 (9)	6.0	718	
090112A	59±43	214 (25)	11.7±0.7 (19)		6.2	1478	
090114A	68±130	811 (42)			6.1	1335	1515
090114B	123±106	389 (22)		14.6±5.2 (21)	6.0	1429	1272
090116A	48±38	200 (41)	10.9±0.7 (12)		5.8	1067	887
090116B	94±107	476 (16)		14.7±3.0 (17)	6.2	609	900
090118A	66±76	273 (26)	13.6±0.8 (8)		5.7	913	794
090118B	122±150	788 (74)		11.0±3.5 (55)	5.8	4425	4619
090120A	55±50	220 (40)	13.7±0.9 (10)		6.1	1155	1048
090120B	97±102	352 (36)		12.2±5.5 (27)	5.9	1708	1776
090122A	147±191	837 (44)	13.7±0.3 (12)		5.8	3789	2673
090122B	37±24	142 (42)		12.5±4.0 (31)	6.1	558	1013
Grand mean	92	388	12.7	13.0	5.9	1465	

Data are means ± s.d. Numbers in parentheses indicate sample size.

Air and ground speeds were calculated only for relatively long flights (>30 s).

a grand mean dive duration of 110 s (max. 306 s) for males and 53 s (max. 154 s) for females (Table 4). Males dived significantly deeper (GLMM, $\chi^2=7.5$, $P<0.01$, $N=4084$) and for longer durations (GLMM, $\chi^2=7.9$, $P<0.005$, $N=4084$) than females.

GPS position, depth and acceleration were simultaneously recorded for six birds, providing the tracks of foraging trips and the records of diving behaviour. Dive depths were generally consistent with the local sea depth, although some dives were much shallower (Fig. 4). Each trip consisted of the periods of flight, stay at the sea surface and diving (Fig. 5), with the maximum distance from the colony ranging from 1.4 to 26.2 km (Table 1). Flights were not always followed by diving interrupted by a surface period, but were often followed by another flight interrupted by a surface period. This flight–surfacing–flight sequence was observed even when the birds were heading directly back to the colony (Fig. 5). Based on the acceleration data from 25 birds, 206 of 695 flights (29%) were followed by another flight rather than diving interrupted by a surface period. In these flight–surfacing–flight sequences, the duration of the first flight was positively related to the subsequent surface duration (GLMM, $\chi^2=21.0$, $P<0.0001$; Fig. 6).

According to the Pennycuik model (Pennycuik, 2008), the values of V_{mp} and V_{mr} of Kerguelen shags were 13.2 and 19.8 m s⁻¹, with the mechanical power required equal to 39 and 47 W, respectively. The observed speeds agreed well with V_{mp} , and were much lower than V_{mr} (Fig. 3). According to the Norberg model (Norberg, 1990), the values of V_{mp} and V_{mr} were 11.3 and 15.2 m s⁻¹, with the mechanical power required equal to 28 and 33 W, respectively. The observed speeds agreed better with V_{mp} than with V_{mr} , although the difference was less clear than in the Pennycuik model (Pennycuik, 2008).

DISCUSSION

Direct measurement of flight air speed

The power requirement for flapping flight is high and is directly affected by air speed (Norberg, 1990; Pennycuik, 2008). Therefore, recording flight air speed is important not only in biomechanics but also in the ecology of flying animals (Hedenstrom and Alerstam, 1995). We provided, to our knowledge, the first direct measurement

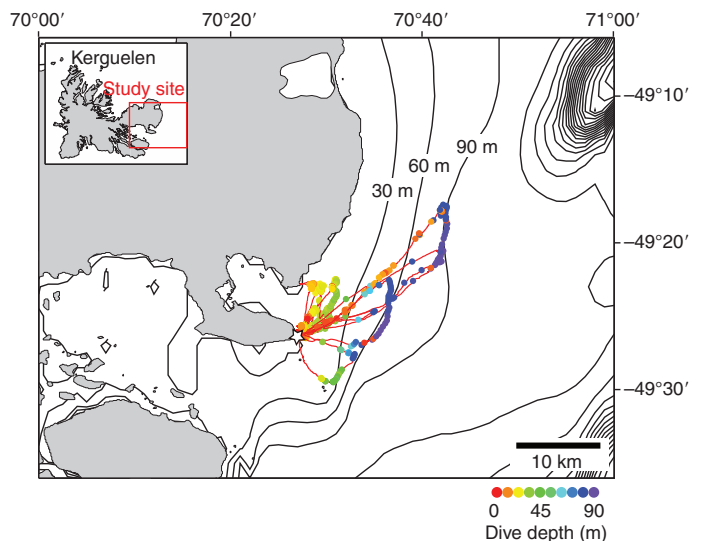


Fig. 4. GPS tracks of six Kerguelen shags, with the location and depth of dives (colour circles) overlaid on the bathymetric map. The star indicates the location of the colony.

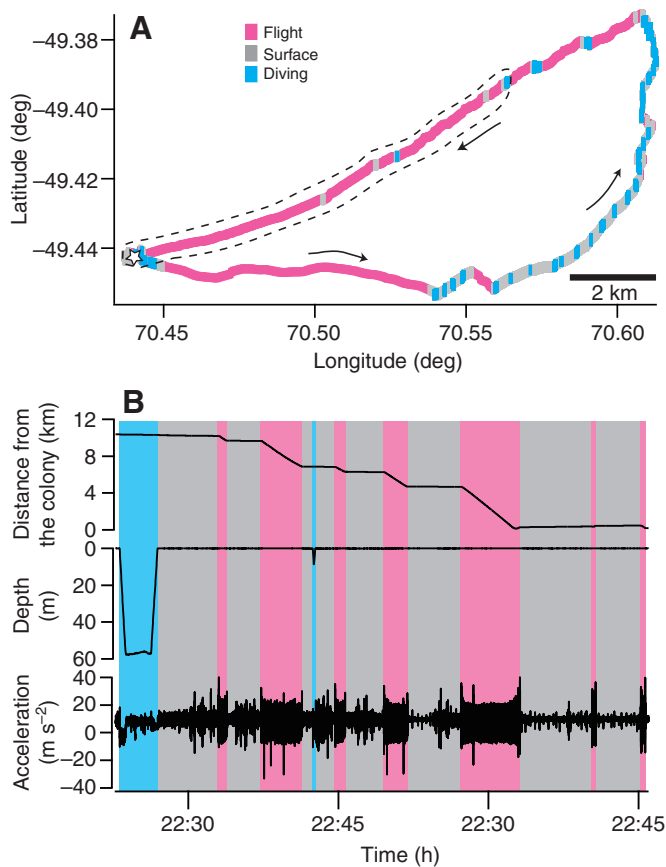


Fig. 5. (A) GPS track of a foraging trip made by a Kerguelen shag (bird ID: 090120B), with behavioural categories including flight (pink), stay at the sea surface (grey), and diving (blue). The star indicates the location of the colony. (B) Time-series data (distance from the colony, depth and dorso-ventral acceleration) on the way back to the colony, including the last deep dive (the part of the GPS track shown by the dashed line in A). Note that the bird stayed at the surface without diving between flights, which is suggestive of resting. Colour codes are as in A.

of flight air speed in wild birds. According to the calibration experiments using the wind tunnel, the range of air speed that can be measured with our propeller loggers was between 6 and 21 m s⁻¹, which covers the normal speed of most flying birds (Welham, 1994; Bruderer and Boldt, 2001; Alerstam et al., 2007). Although we have no independent data to validate the field measurement of flight air speed, similar mean values of air and ground speed during flights suggest that our measurement is reasonable. This is because the shags made return foraging trips from the colony (see Fig. 5), and hence the effect of wind (which is shown by the difference between air and ground speed) during the trips is expected to sum to zero.

Our method using propeller loggers has several advantages over conventional ground-based methods, in which flight speed relative to the ground is measured using stopwatches (Elliott and Gaston, 2005), radar (Alerstam et al., 2007), theodolites (Pennycuik, 2008) or hydrophone arrays, e.g. in bats (Grodzinski et al., 2009), and then wind speed is subtracted to obtain air speed. First, our method does not require information on the speed and direction of the wind experienced by the animals, which is difficult to measure. Second, it does not require the animals to fly closely to the observers, and hence air speed can be recorded continuously for long periods. Third, our propeller loggers provide data on several behavioural parameters,

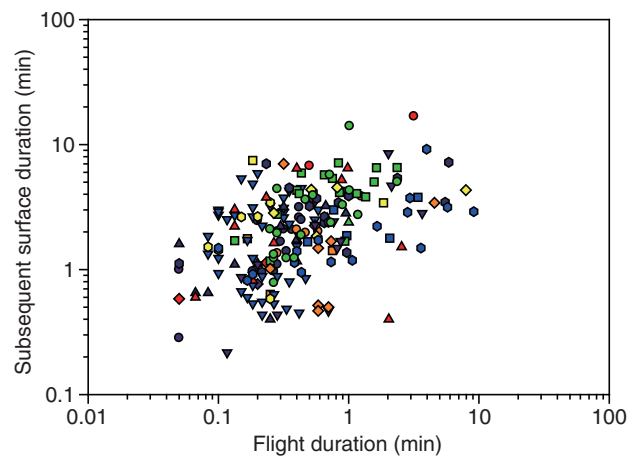


Fig. 6. Relationship between flight duration and the subsequent surface duration of the flight–surfacing–flight sequences during foraging trips in 25 Kerguelen shags. Different symbol–colour combinations represent different individuals.

such as acceleration, in addition to flight air speed. However, the size of the propeller logger (60 g) is currently limiting its application to relatively large birds. Nevertheless, this method has a great potential in the studies of flying animals.

Flight and diving capability

According to the Pennycuik model (Pennycuik, 2008), the minimum mechanical power required for flight (i.e. the power at V_{mp}) was 39 W in Kerguelen shags. Independently, the maximum aerobically sustainable mechanical power available for flight in a 2.3 kg shag can be estimated to be 39 W, by assuming that the bird has flight muscles equal to 17% body mass (Bishop and Butler, 1995) and that 1 kg of flight muscle generates the maximum mechanical power of 100 W (Marden, 1994). Similar estimates of the power required (39 W) and the power available (39 W) suggest that the flight of Kerguelen shags is near the limit of aerobic metabolism. According to the Norberg model (Norberg, 1990), the minimum mechanical power required is 28 W, which is less than the estimate for the mechanical power available (39 W), suggesting that shags have enough aerobic power to fly at least at V_{mp} . Nevertheless, their flight speed is predicted to be limited to <17.3 m s⁻¹, above which the power required exceeds the power available. Overall, these analyses suggest that Kerguelen shags do not have a large margin of power available relative to the power required during flight, and that their flight capabilities are physiologically limited. These analyses might be an oversimplification, because: (1) there are inevitable uncertainties in the aerodynamic models (Rayner, 1999), and (2) the mass-specific mechanical power of flight muscles might change depending on several factors, including wing kinematics, flight speed, body size (Tobalske, 2007) and the composition of muscle fibres (Bishop, 2005). However, as shown below, our empirical data on the free-ranging flight behaviour support the suggestion.

Flight duration was only 92 s on average, which means that shags flew only ~1 km during each flight at a mean ground speed of 13 m s⁻¹. The sum of flight durations in a day was only 0.4 h on average, which is similar to the value of the common eider *Somateria mollissima* (0.2 h d⁻¹) (Pelletier et al., 2008), a large sea duck that is presumably at the limit of flight capability (Guillemette and Ouellet, 2005). Most birds fly for a longer daily duration, with

Table 4. Diving behaviour of Kerguelen shags

Individual	Dive depth (m)		Dive duration (s)		Swim speed (m s ⁻¹)		Total dive duration (s day ⁻¹)	
	Mean	Max.	Mean	Max.	Descent	Ascent	Day 1	Day 2
081223A	32.5±23.9	58.4 (19)	116±88	215 (19)			2201	
081223B	27.6±21.7	76.7 (104)	89±69	270 (104)			9254	
081224A	1.9±0.9	5.0 (331)	27±7	45 (331)			8811	
081224B	17.8±4.8	23.9 (142)	90±30	154 (142)			12855	
081226A	31.8±10.9	41.4 (57)	135±50	208 (57)			7680	
081226B	11.9±9.2	25.0 (95)	64±50	145 (95)	1.48±0.03 (42)	1.56±0.06 (42)	6096	
090101A	16.7±3.8	23.9 (180)	66±18	111 (180)	1.35±0.11 (32)	1.56±0.18 (32)	11848	
090101B	2.0±1.0	8.0 (625)	14±8	44 (625)			7047	1416
090105A	48.7±20.5	79.8 (58)	171±73	261 (58)	1.54±0.24 (47)	1.64±0.18 (47)	4601	5334
090105B	26.3±27.7	74.0 (124)	95±89	256 (124)	1.49±0.08 (40)	1.51±0.13 (40)	5313	6459
090106	14.4±27.8	94.2 (184)	51±81	285 (184)			9403	
090110A	24.2±12.4	35.3 (166)	105±55	194 (166)	1.63±0.08 (92)	1.69±0.11 (92)	8639	8810
090110B	16.5±7.6	24.3 (172)	92±40	144 (172)	1.43±0.06 (99)	1.60±0.10 (99)	8911	6951
090110C								
090111	21.1±11.4	31.1 (65)	96±50	154 (65)			6228	
090112A	13.8±8.7	26.0 (179)	70±45	125 (179)			12610	
090114A	14.0±23.0	81.3 (307)	57±79	286 (307)	1.52±0.09 (45)	1.67±0.10 (45)	11495	5913
090114B	18.7±4.8	28.5 (153)	92±22	148 (153)			5764	8382
090116A	18.7±4.8	28.3 (193)	90±29	140 (193)			8542	8802
090116B	20.6±7.1	31.9 (173)	113±41	187 (173)			6619	12934
090118A	23.1±8.0	29.2 (88)	124±50	172 (88)			6946	3933
090118B	40.7±37.2	91.8 (143)	130±113	291 (143)			6806	11848
090120A	18.5±8.3	29.8 (232)	68±36	152 (232)			8947	6792
090120B	51.3±28.4	90.8 (94)	177±92	306 (94)			7734	8893
090122A	65.6±20.5	84.9 (72)	234±64	296 (72)	1.56±0.02 (33)	1.52±0.12 (33)	7718	9124
090122B	10.3±5.5	16.7 (128)	51±25	95 (128)			2902	3650
Grand mean	23.5	45.6	97	187	1.50	1.59	7824	

Data are means ± s.d. Numbers in parentheses indicate sample size.

a mean value of 4.1 h d⁻¹ (Pelletier et al., 2008), although available information is limited. Note, however, that short flights do not necessarily indicate poor flight capability, because shags may not need to fly longer because of the presence of prey near the colony. According to the simultaneous records of GPS position, depth and acceleration, the shags sometimes stayed at the sea surface without any diving activity between flights, even when they were headed directly back to the colony. In such flight–surfacing–flight sequences, the duration of the first flight was positively related to the subsequent surface duration. These observations suggest that surfacing periods have a function of rest, and that longer flights require longer surfacing periods. This is analogous to the observations of breath-hold diving animals, where longer dives require longer surfacing periods, especially when anaerobic metabolism is incorporated during the dives (Kooyman, 1989). Thus, the short flight durations in the shags are likely due to their physiological limitations, rather than their environment.

Moreover, the measured flight air speeds were close to V_{mp} and lower than V_{mr} , especially when the Pennycuik model (Pennycuik, 2008) was applied. The Norberg model (Norberg, 1990) produced a steeper flight power curve (where high speed is very expensive) and hence lower V_{mr} . This difference is expected from the different assumption for profile power, which is proportional to speed cubed in the Norberg model (Norberg, 1990) (Eqn 6) and is speed-independent in the Pennycuik model (Pennycuik, 2008) (Eqn 5). Our observation of flight speed close to V_{mp} contrasts with optimal flight theories, which predict that birds feeding chicks (as the shags in this study) should fly faster than V_{mr} to maximize energy delivered to the chicks (Norberg, 1981; Hedenstrom and Alerstam, 1995). Instead, our observation agrees with the suggestion that shags do not have a large margin of power available relative to the power

required during flight. Flight at V_{mp} was presumably the practical choice for the shags without relying heavily on anaerobic metabolism, compared with V_{mr} , which requires higher power. A similar suggestion was previously made for the European shag *P. aristotelis*, based on the flight speed measured by theodolites (Pennycuik, 1987). Our results may be due to the negative effect of the logger attached; however, note that we included the mass and frontal area of the loggers in the power curve calculation, which means that the device effect was accounted for, although the possible increase in drag coefficient (resulting from the change in the body outline) could not be ruled out. Overall, our behavioural and biomechanical analyses support the prediction that flight performance is limited in Kerguelen shags.

By contrast, their diving performance was remarkable. The maximum recorded dive depth (94 m) and duration (306 s) are similar to the previous records of the same species and other blue-eyed shags, and are much greater than those of non-blue-eyed cormorants (Quintana et al., 2007; Cook et al., 2008). These values are close to the records of penguins, when the effect of size is accounted for (Schreer and Kovacs, 1997). A large variation in dive depth among individuals and between sexes (Table 4) is clearly explained by the variation in depth of the foraging sites: individuals foraging at the deeper coastal area dived deeper (Fig. 4). This is consistent with observations that Kerguelen shags prey on benthic animals, including nototheniid fishes (T. R. Cook, C.-A.B. and Y. Cherel, unpublished) and polychaetes (Y.Y.W. and C.-A.B. unpublished).

The compromise

The contrasting performances of flight and diving in Kerguelen shags are presumably interrelated through their morphological characteristics. First, Kerguelen shags are large (mean 2.3 kg) among

seabirds that exhibit flapping flight. Large body mass is disadvantageous for flapping flight, because power requirement increases with size more rapidly than the power available (Pennycuik, 2008). By contrast, it is advantageous for breath-hold diving, because oxygen storage capacity increases with size more rapidly than the rate of oxygen metabolism, enabling larger animals to dive deeper and longer (Halsey et al., 2006). Second, the wings of cormorants are characterized by a low aspect ratio (7.6 in this study) and a short wingspan (1.2 m in this study) for their size among seabirds (Gaston, 2004). A different expression for this characteristic is a high wing loading for their size (127 N m^{-2} in this study), although auks have higher wing loading for their size (Gaston, 2004). Short wings are disadvantageous for flapping flight because of increased induced power (see Eqn 3). By contrast, short wings are advantageous for diving, because they decrease the magnitude of positive buoyancy (because of decreased air volume in the feathers) and drag (because of decreased body surface area) in the water, and hence the cost of swimming (Wilson et al., 1992; Wilson et al., 2008). Third, the flight muscles of cormorants are small among flying birds (17% of body mass) (Bishop and Butler, 1995), limiting the power available for flight. This is presumably related to their large leg muscles (10–12% body mass, compared with 4.5–5.5% in non-diving pelicans) (Nelson, 2005), which provides power for swimming. In foot-propelled swimmers, such as cormorants, loons, grebes and ducks, different muscles are used for flight and swimming, and flight and leg muscles cannot be equally powerful while maintaining body size. Wing-propelled swimming, observed in auks, diving petrels and some shearwaters, is an evolutionary solution for the conflict of muscle allocation; however, these birds face other conflicts, including the design of wings (which cannot be efficient in both air and water) (Pennycuik, 2008) and the myoglobin concentration in the locomotor muscles (Croll et al., 1992; Davis and Guderley, 1987).

Our results have implications for the ecology and evolution of seabirds. First, the compromise between flight and diving might be a major factor in determining their three-dimensional foraging range, with horizontal and vertical components limited by flight and diving capability, respectively. Poor flyers have a limited horizontal foraging range, which might be compensated by their great diving capability, and *vice versa*. Note, however, that such relationship is mediated by the local bathymetry in bottom-feeders, such as Kerguelen shags. Because of the shallow bathymetry of the Kerguelen archipelago and the great diving capability of Kerguelen shags, a relatively large horizontal area (<26 km offshore from the colony) with respect to their limited flight capability was utilised by the shags (Fig. 4). Second, an extreme of the compromise between flight and diving would be flightless birds with enhanced diving capability, which is in fact found in Galápagos cormorants (Wilson et al., 2008). Our empirical data on deep-diving seabirds capable of flight agree with the results of Wilson et al. (Wilson et al., 2008), which suggest that giving up flight ability prompted the evolution of great diving capability in Galápagos cormorants.

In conclusion, we provided detailed records of flight behaviour in Kerguelen shags, including the first direct measurement of flight air speed using propeller loggers. Their flight performance was poor, as indicated by: (1) short flight duration; (2) surfacing behaviour between flight events, suggestive of resting, with the positive relationship between flight duration and subsequent surface duration; and (3) flight air speed close to the theoretical V_{mp} rather than V_{mr} . These results are presumably related to the great diving capability of Kerguelen shags through their morphological adaptations for diving, including large body mass, small flight muscles and short wings. The compromise between flight and diving, and the local

bathymetry, shape the three-dimensional foraging range in this bottom-feeding cormorant.

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