

Flight speeds of two seabirds: a test of Norberg's hypothesis

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Norberg suggested that birds should increase their flight speed when rearing chicks in order to maximize chick energy intake by reducing commuting time. We measured the incubation and chick-rearing flight speeds of a medium-range (Brünnich's Guillemot *Uria lomvia*) and long-range (Northern Fulmar *Fulmarus glacialis*) forager near the Prince Leopold Island colony, Nunavut, Canada. The mean flight speed for the long-range forager was significantly higher during chick-rearing than during incubation. The medium-range forager showed no difference in mean flight speed during the two periods. We suggest that because petrels fly close to their minimum power velocity and have a low wing-loading, whereas alcids fly close to their maximum range velocity and have a high wing-loading, petrels have a greater ability than alcids to alter their flight speed according to changes in the demands of different breeding stages. Consequently, whereas Northern Fulmars adapt to the additional cost of chick-rearing partially by altering flight speed, Brünnich's Guillemots can only do so by reducing mass.

Aerodynamic theories of powered flight allow for the calculation of the flight energy costs in relation to speed (e.g. Tucker 1973, Rayner 1979, 1993, Pennycuick 1995, 1998). Such calculations predict a U-shaped total power curve and specify velocities where energy spent per time in air (minimum power speed, V_{mp}) or distance travelled (maximum range speed, V_{mr}) is minimized (Rayner 2001). Recent laboratory studies have verified that the aerodynamic power used by several species is consistent with theoretical models (Dial *et al.* 1997, Ward *et al.* 2001, Tobalske *et al.* 2003). However, there is still debate over the metabolic power needed for bird flight (Ellington 1991, Pennycuick 1995, Alexander 1997, Rayner 1999, 2001). Despite these limitations, aerodynamic models are believed to give realistic estimates of power use in the field (Pennycuick 1998, Rayner 1999, 2001).

There are many flight speeds that may optimize avian fitness in the long term (Pyke 1981, Hedenstrom & Alerstam 1995). However, most researchers have focused on V_{mp} and V_{mr} , as they do not depend on energy intake, a difficult parameter to estimate in the field. Most seabirds fly at a speed intermediate between V_{mp} and V_{mr} , based on conventional values for the parasite drag coefficient (Schnell & Hellack

1979, Pennycuick 1987, Mordvinov 1992, Spear & Ainley 1997). Recent studies suggest a lower value for the parasite drag coefficient, and re-analysis of the field studies with this drag coefficient suggest that no seabird flies faster than V_{mr} (Pennycuick 1997, 1998, Rayner 1999, 2001).

Norberg (1981a) showed that in order to maximize the energy delivered to nestlings, a parent bird must fly faster than V_{mr} when rearing nestlings. In order to maximize net energy gain per unit time, including travel time, Norberg predicted that central place foragers must fly faster than V_{mr} provided that the energy gained in extra foraging time outweighs the travel cost. He showed that the optimum speed, V_{Nor} , is the speed at which the slope of the 'compound power curve' (the flight power curve increased by P_g , the rate of energy accumulation during foraging) matches the slope of a line through the origin. However, Norberg adds that his hypothesis is particularly amenable to field studies because it 'is testable without knowledge of the bird's power-vs.-speed curve or its maximum-range speed' (Norberg 1981a). Qualitatively, assuming that parents wish to maximize the rate of delivery to offspring, Norberg's model predicts that birds should fly faster when rearing nestlings.

Elliott *et al.* (2004) detected no difference in the flight speed of Marbled Murrelets *Brachyramphus*

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marmoratus during incubation, chick-rearing and non-breeding. However, there are several other aspects of Marbled Murrelet flight kinematics that are unusual, and probably due to their adaptation for long-distance flights to nest-sites in old-growth forests (Elliott *et al.* 2004). McLaughlin and Montgomerie (1985) detected no significant difference in flight speeds of female Lapland Longspurs *Calcarius lapponicus* feeding nestlings compared with those incubating, and concluded that both flight speeds were below V_{mr} . Nevertheless, they suggested that there may be an energetic advantage to speeds greater than V_{mr} during chick-rearing for Brünnich's Guillemots *Uria lomvia* and petrels, which make longer foraging trips.

Seabirds are ideal candidates for testing Norberg's hypothesis because they commute very long distances in order to forage. Brünnich's Guillemots nesting at Prince Leopold Island, Nunavut, Canada, regularly commute a round trip of more than 100 km, and Northern Fulmars *Fulmarus glacialis* up to 500 km (Gaston & Nettleship 1981). Guillemot chicks fledge before completing their growth, which is probably because the adults cannot maintain the large energetic cost of feeding them beyond this point (Gaston & Nettleship 1981, Ydenberg 1989). Fulmars cease brooding their chicks after about 2 weeks, suggesting that feeding time constraints are also important in this species. Consequently, we would expect that these two species are under considerable selective pressure to maximize chick growth rates and that Brünnich's Guillemots and Northern Fulmars would fly faster during chick-rearing than during incubation.

METHODS

We set up two markers 850 m apart, using infrared distance-sensing binoculars, accurate to within 10 m, along the edge of a gravel spit south of the main colony at Prince Leopold Island (74°00'N, 89°50'W). Both Fulmars and Guillemots regularly flew on a straight course between these markers, as they followed the edge of the spit to or from their feeding grounds. Both species flew directly to or from the colony and in the direction of or from major feeding grounds, and we therefore assumed that these flights were typical foraging flights. We measured on a wristwatch the time taken between markers, from a viewpoint 300 m above the spit. The first marker was 150 m along the spit from the base of the viewpoint, whereas the second marker was 1 km from the base of the viewpoint.

Wind is always a significant source of error in field observations of flight speeds, as the wind cannot be measured at the exact time and place where the bird is flying. We minimized uncertainty associated with wind speed by only measuring flight speeds on days when no wind was detected on a hand-held anemometer, and there were no visible ripples on the water adjacent to the spit. We only timed individuals in level flight and along a flight path that avoided potential updrafts. An observer was present on the spit during about 10% of the total observations, and confirmed that the birds observed were travelling in level flight, within 5 m (Brünnich's Guillemots) or 3 m (Northern Fulmars) of the ground, and that the observer at the viewpoint correctly judged, within 10 m, the time when they passed each marker. The observer on the spit, equipped with 8× binoculars, was halfway between the two markers, and about 250 m from the flight path taken by the birds. Assuming an accuracy of 0.5 m/s for the wind speed (the minimum measurement on the anemometer), 30 m for the distance travelled (this assumes 10 m accuracy for the total distance measurement, and 10 m for errors due to parallax at each end, as corroborated in the subset of measurements with an observer on the ground), and an accuracy of 1 s on timing the flights (the time between when the bird was judged to pass the marker and when the 'stop' or 'start' button was pressed was always less than 0.5 s), we calculated an absolute error of approximately 1 m/s for individual measurements of Brünnich's Guillemot and 0.7 m/s for Northern Fulmars.

To estimate power curves we use Pennycuick's model (Pennycuick 1998)

$$P(V) = R \left(\frac{P_{aer}}{\eta} + P_{br} \right)$$

$$P_{aer} = \frac{2kM^2g^2}{\pi b^2 \rho V} + \frac{1}{2} \rho S_b C_{Dpar} V^3$$

$$+ 4^{5/4} 3^{-3/4} k^{3/4} C_2 \frac{S}{b^2} \frac{(Mg)^{3/2} (S_b C_{Dpar})}{\pi^{3/4} \rho^{1/4} b^{3/2}}$$

with the default parameters (Pennycuick 1995, 1998) $R = 1.1$, $\eta = 0.23$, $k = 1.2$, $\rho = 1.23 \text{ kg/m}^3$, $g = 9.81 \text{ m/s}^2$, $C_{Dpar} = 0.1$ and $C_2 = 8.4$. Of the remaining variables, we measured the mass (M) of birds of known breeding status at Prince Leopold Island (Table 1), we calculated the basal metabolic rate ($P_{br} = 5 \text{ W}$, Guillemots; 4 W , Fulmars) from the equations given by Mehlum *et al.* (1993), and we obtained wingspan ($b = 0.72 \text{ m}$, Guillemots; 1.13 m , Fulmars), cross-sectional area ($S_b = 90 \text{ cm}^2$, Guillemots; 78 cm^2 ,

Table 1. Mean mass of breeding Northern Fulmars and Brünnich's Guillemots on Prince Leopold Island in 2002 (sample sizes in parentheses). Individuals were captured at the nest-site, weighed and released.

	Northern Fulmar		Brünnich's Guillemot	
	Mean	sd	Mean	sd
Incubating	713.7 (88)	104.3	887.5 (53)	62.8
Brooding	659.2 (18)	93.4	840.2 (32)	64.6
<i>t</i>	2.21		3.30	
<i>P</i>	0.03		0.001	

Fulmars) and wing area ($S = 550 \text{ cm}^2$, Guillemots; 1240 cm^2 , Fulmars) from the literature (Croll *et al.* 1991 for Guillemots; Pennycuick 1997 for Fulmars). We estimated the average rate of energy accumulation, P_g , to be about 20 W for Guillemots and 15 W for Fulmars, based on average energy intake per day (Gaston & Nettleship 1981). We used Newton's method to solve for V_{mr} based on the following equation:

$$P(V) = \frac{dP(V)}{dV} V.$$

We used the same equation to estimate V_{Nor} , but with $P(V)$ increased by P_g . Error bars and uncertainty estimates for $P(V)$ and V_{mr} follow Spedding and Pennycuick (2001). Although there is considerable debate over the values of several of these parameters, particularly C_{Dpar} , η and the profile drag (third term in P_{aer}), the Pennycuick model is the most widely used in the literature and likely to give realistic estimates for the field (Pennycuick 1995, 1998, Rayner 1999, 2001). We calculated the mass-specific maximal energy output based on Askew *et al.* (2001) and Pennycuick (1997) as 45 kJ/kg.

Chick-rearing and incubation periods were determined from daily plot surveys using methods outlined by Gaston and Nettleship (1981), and we only measured flight speeds when there was no overlap between the two periods; all birds on the surveyed plots were either incubating or chick-rearing. However, the actual breeding status of individuals for which flight speeds were measured was not known; presumably some birds were non-breeders. Statistical tests were completed using MS Excel 2000. A two-tailed *t*-test was employed after testing for normality. All flight speeds are presented as means \pm 1 sd. If each individual flies at its 'optimal speed', the speed range observed reflects the range of morphometric, physiological and behavioural parameters present in the population and we can therefore com-

pare the average speed measured to the calculated V_{mr} and V_{Nor} , based on the parameters of an 'average' bird (presumably 'optimal decision rules' represent average decisions for a population, with some individuals choosing other decision rules based on their current conditions).

RESULTS

The flight speed of Brünnich's Guillemots was $20.1 \pm 1.8 \text{ m/s}$ ($n = 105$, Fig. 1), with no significant difference between the incubation (20.5 m/s, Table 2) and chick-rearing periods (19.9 m/s). We therefore found no support for Norberg's hypothesis for this species. The flight speed of Northern Fulmars was significantly lower during incubation (9.2 m/s, Table 2) than during chick-rearing (10.8 m/s; Fig. 2), a result consistent with Norberg's hypothesis. This difference was greater than the estimated uncertainty in our flight-speed measurements (1 m/s).

There was no significant difference between the flight speeds of incoming and outgoing Brünnich's

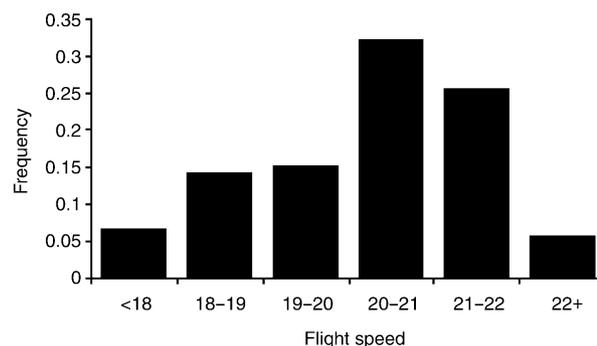


Figure 1. Distribution of flight speeds (m/s^{-1}) for Brünnich's Guillemot.

Table 2. Flight speeds (m/s^{-1}) recorded for Brünnich's Guillemots and Northern Fulmars during two stages of breeding.

	Brünnich's Guillemot		Northern Fulmar	
	Mean \pm sd	<i>n</i>	Mean \pm sd	<i>n</i>
Incubation	20.5 ± 1.8	33	9.2 ± 1.2	101
Chick-rearing	19.9 ± 1.8	72	10.8 ± 1.2	106
<i>t</i>	1.75		-9.24	
<i>P</i>	0.08		< 0.001	
Incoming	20.3 ± 1.7	49	10.2 ± 1.2	164
Outgoing	19.8 ± 1.9	56	8.8 ± 1.5	18
<i>t</i>	1.46		4.58	
<i>P</i>	0.15		< 0.001	

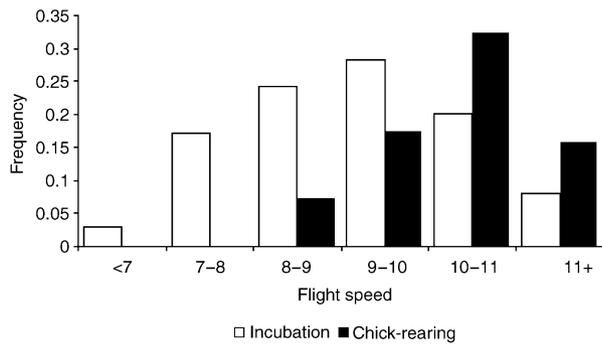


Figure 2. Distribution of flight speeds (m/s^{-1}) for Northern Fulmars during chick-rearing and incubation.

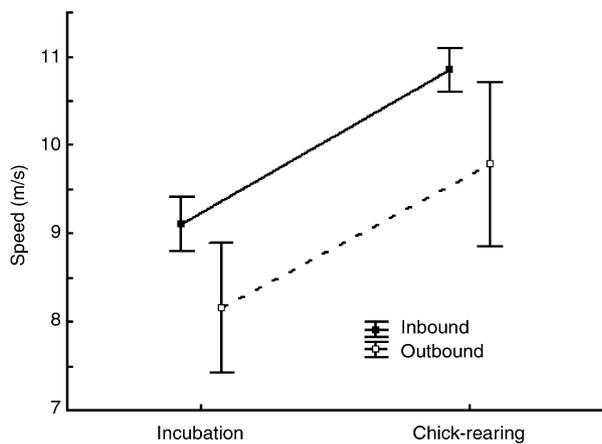


Figure 3. Flight speeds of incoming and outgoing Northern Fulmars during the incubation and chick-rearing periods (mean \pm 1 sd).

Guillemots (Table 2, Fig. 1). The flight speed of Northern Fulmars was significantly lower for outgoing birds (8.8 m/s, Table 1) than for incoming birds (10.2 m/s, Fig. 3). This difference was again greater than the estimated uncertainty in our flight-speed measurements. A two-way factorial ANOVA suggested

that both breeding stage and flight direction had significant effects on flight speed, but there was no interaction between variables ($F_{3,168} = 34.8, P < 0.001$). Flight speeds of inbound birds were significantly higher than those of outbound birds during both incubation and chick-rearing periods (Fig. 3), but the speed of inbound birds during the incubation period did not differ from the speed of outbound birds during chick-rearing. Our flight speeds were similar to those found by other observers, including measurements well away from any colony (Table 3; Pennycuik 1987), and we therefore concluded that they were representative of average commute speeds between foraging sites and the colony, and not influenced by a 'colony effect'.

Using the Pennycuik model, we calculated V_{mr} as 16.0 ± 2.3 m/s (Northern Fulmar, incubating), 15.5 ± 2.1 m/s (Northern Fulmar, chick-rearing), 20.7 ± 0.9 m/s (Brünnich's Guillemot, incubating) and 20.2 ± 0.9 m/s (Brünnich's Guillemot, chick-rearing) and V_{Nor} as 18.7 ± 2.9 m/s (Northern Fulmar, chick-rearing) and 22.4 ± 1.0 m/s (Brünnich's Guillemot, chick-rearing). Thus, Northern Fulmar flight speeds were below V_{mr} (incubating, $z = 2.36, P = 0.02$; chick-rearing $z = 2.10, P = 0.04$) and Brünnich's Guillemot flight speeds did not differ significantly from V_{mr} (incubating, $z = 0.08, P = 0.93$; chick-rearing, $z = 0.14, P = 0.08$). Chick-rearing Northern Fulmar flight speeds were also below V_{Nor} ($z = -3.90, P < 0.001$) while Brünnich's Guillemot did not differ from V_{Nor} ($z = -1.49, P = 0.14$). As can be seen by comparing Figures 1 and 2 with Figure 4, both Northern Fulmars and Brünnich's Guillemots have a wide power margin over the range of speeds they actually use in the field. This is important because Norberg's model assumes that individuals are not limited by the power available, and are actually able to increase their speed to V_{Nor} . We can therefore assume that their actual speed range reflects the smaller range of speeds that are economical.

Table 3. Reported Guillemot flight speeds (locations with an asterisk refer to Common Guillemots; the remainder are for Brünnich's Guillemot).

Location	Method	Source	Mean speed (ms^{-1})
Coats Island, NU	Stopwatch over known distance	Croll <i>et al.</i> (1991)	20.9
Iceland	Data logger	Benvenuti <i>et al.</i> (1998)	18.1
Prince Leopold Island, NU	Stopwatch over known distance	Present study	20.1
Britain*	Stopwatch over known distance	Vaughan (1937)	22
Britain*	Stopwatch over known distance	Salomonsen (1950)	18
Britain*	Ornithodolite	Pennycuik (1987)	19.1
Russia*	Stopwatch over known distance	Mordvinov (1992)	19.4

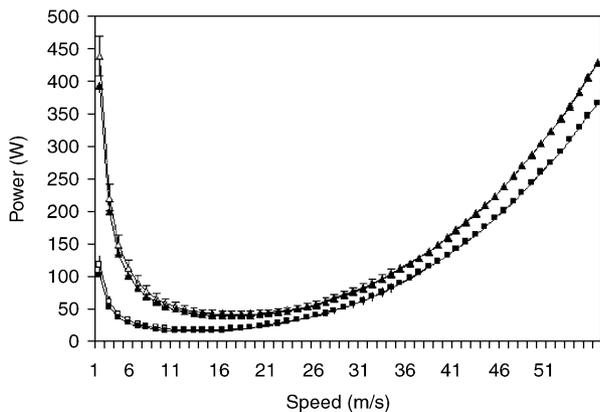


Figure 4. Power curve for Guillemots during incubation (open triangles) and brooding (closed triangles) and for Fulmars during incubation (open squares) and brooding (closed squares), based on the Pennycuik (1998) model. Error bars are based on the formulae in Spedding and Pennycuik (2001). The Pennycuik model is based on wind-tunnel experimentation between V_{mp} and V_{mr} ; extrapolations outside this range must be made with care. For clarity, we only show error bars for incubating birds for each species. Lines represent the maximal power output based on Askew *et al.* (2001) and Pennycuik (1997).

DISCUSSION

Our results suggest that Northern Fulmars fly faster during chick-rearing than during incubation, but Brünnich's Guillemots do not. We conclude that Fulmars optimize their flight speed according to Norberg's hypothesis whereas Guillemots do not. Although our results do not agree quantitatively with Norberg's hypothesis for either species, our estimate for V_{Nor} depends heavily on several model parameters, particularly C_{Dpar} , η and P_g , which are poorly known. Consequently, our estimate should be considered rough at best. Although our estimates for V_{mr} and V_{mp} are subject to similar limitations, they suggest that Guillemots fly at approximately V_{mr} while Fulmars fly closer to their V_{mp} .

It is possible that our Fulmar flight speeds were below V_{mr} due to calm wind conditions. Flight costs are higher for Fulmars during calm weather because in the absence of wind they must use flapping rather than gliding flight (Furness & Bryant 1996). As we only measured flight speeds during calm weather, and during our observations Fulmars used flapping flight almost exclusively, it is possible that they minimized power during calm weather in anticipation that faster flight speeds could be obtained at lower cost during windier weather. Furthermore, because

optimal gliding speeds are determined largely by wind speed (Furness & Bryant 1996), Fulmars may not be as flexible with their flight behaviour during windier conditions, and Norberg's hypothesis may not hold true on windy days.

We suggest three reasons why Fulmars optimize their flight speed according to Norberg's hypothesis on calm days, but Guillemots do not. First, because Guillemots are already flying at a speed close to V_{mr} , additional increases to flight speed are proportionately more costly for this species than for Fulmars, which fly at speeds where their power curve is flatter (Fig. 4). Although speeds greater than V_{mr} , such as V_{Nor} , may optimize energy delivered to the nestling, they may create negative side-effects, such as muscle damage (Guglielmo *et al.* 2001). Secondly, because Fulmars have a much lower wing loading than Guillemots, cost of flight is lower and their power curve is flatter (Fig. 4). Consequently, increases to flight speed are less costly for Fulmars than for Guillemots. Thirdly, Guillemots not only fly faster than Fulmars, they also have a much higher wing-beat frequency. For many species there is an optimal combination of wing-beat kinematics and flight speed (Ward *et al.* 2001, Taylor *et al.* 2003), and changes to Guillemot flight speed may involve substantial changes to the wing-beat kinematics not incorporated by the power curve.

Fulmars lose up to 15% of their mass during incubation shifts and carry up to 15% of their mass in food upon returning to the colony to feed their chicks (Hatch & Nettleship 1998, A.J.G. and S. Jacobs unpubl. data). Consequently, at both breeding stages, birds leaving the colony weigh substantially less than those returning to the colony. According to the Pennycuik model, this mass difference would cause a 1.0 ± 1.5 m/s decrease in V_{mr} while the actual difference observed was a significant decrease of 1.4 ± 1.9 m/s. Thus, our results suggest that Fulmars alter their flight speed in response to changes in mass. Nudds and Bryant (2002) also found a behavioural change in response to increased load in Zebra Finches *Taeniopygia guttata*, although in their study the birds flew more slowly with increased load. Clearly much is yet to be learned about the effect of increased body mass on flight energetics and behaviour (Gessaman & Nagy 1988, Kvist *et al.* 2001). Brünnich's Guillemots, which do not carry as large a food load as Fulmars and have much shorter incubation shifts (Hatch & Nettleship 1998; Gaston & Hipfner 2000), presumably differ in mass much less between outgoing and incoming flights. Hence, it is

not surprising that there was little difference between outgoing and incoming flight speeds in Brünnich's Guillemots.

Brünnich's Guillemots lose about 5% of their mass prior to chick-rearing, perhaps as an adaptation to reduce the cost of flight during the chick-rearing period (Table 1; Croll *et al.* 1991, Gaston & Perin 1993). Lower mass would mean a lower V_{mr} , and, in the absence of the Norberg effect, a lower mean flight speed during chick-rearing for this species. Hence, our finding that Guillemot flight speeds did not differ between incubation and chick-rearing suggests that Guillemots were actually adjusting their flight speed upwards relative to V_{mr} during the chick-rearing period. This supports the argument that mass loss reduces the cost of flight during chick-rearing.

Like Brünnich's Guillemots, Northern Fulmars are heavier while incubating than while brooding chicks, the difference being similar to the mass loss over the course of an incubation shift (10–15% body mass, Table 1). Hence, on the basis of mass changes alone and their effects on V_{mr} , we would expect Fulmars to fly faster when flying towards the colony than away from it and to fly faster when inbound during incubation than when inbound during chick-rearing. Our results support the first prediction, but not the second, showing that the change in flight speed that we observed was not simply a response to mass change. The ability of Fulmars to fly faster when lighter indicates that their lower wing-loading, and associated lower cost of flight and flatter U-shaped curve, allows them the flexibility to exploit both options: mass loss and increased flight speed.

The flight speeds of Brünnich's Guillemots and aerodynamically similar Common Guillemots *Uria aalge* have been measured on several occasions (Table 2). There is considerable variation in the measured mean flight speed, implying a greater flexibility in 'optimal' velocity than the current study suggests. In particular, Benvenuti *et al.* (1998) measured a significantly slower flight speed for Brünnich's Guillemots averaged over their entire commuting flight than other studies, which focused on flight speeds near the colony. A central assumption of our research is that the flight speed near the colony is representative of the average speed when commuting, and if the Guillemots are speeding up near the colony this may negate our results. Clearly, much is still to be learned about the optimization of avian flight speeds.

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