Flight energetics of the Marbled Murrelet, Brachyramphus marmoratus

Kyle H. Elliott, Miyako Hewett, Gary W. Kaiser, and Robert W. Blake

Abstract: We measured flight speeds (n = 3000) of Marbled Murrelet, Brachyramphus marmoratus (J.F. Gmelin, 1789), to determine whether flight speeds of an exceptionally fast bird coincide with the maximum-range speeds (V_{mr}) predicted by aerodynamic theory. The mean (± SE) speed of 22.6 ± 0.21 m·s^{-1} was significantly higher than the V_{mr} predicted by four models, using conventional values for the parasitic drag coefficient (C_{D_{par}}). In order for the Penny-cuick model to predict a V_{mr} of 22 m·s^{-1}, a C_{D_{par}} of 0.05, which is lower than any previously reported, is necessary; the other models would need to assume even lower values for C_{D_{par}}. We concluded that the cruising speed of Marbled Murrelets exceeds V_{mr}. Marbled Murrelets may exceed V_{mr} as a result of behavioral decisions, and we examined two behavioural hypotheses: that flight speeds exceed V_{mr} to (1) minimize predation rate and (2) maximize chick growth rate. However, there was no significant difference between flight speeds during high (daylight) and low (darkness) predation periods or between chick-rearing and non-breeding periods. Marbled Murrelets may also appear to fly at a speed that exceeds V_{mr} because the underlying aerodynamic theory is inaccurate for this species. To examine the reliability of aerodynamic theory for Marble Murrelets, we compared measured wingbeat frequencies (f) to those predicted by Penny-cuick’s model. The mean f was significantly lower than the f_{pred} predicted by Penny-cuick’s model, and generally, f = 7.9 m^{-0.22} is a better model for auks than Penny-cuick’s model. In addition, the Strouhal number was particularly low (0.12 ± 0.02). We conclude that the current aerodynamic models are insufficient for an exceptionally fast-flying bird.

Résumé : Nous avons mesuré les vitesses de vol du guillemot marbré, Brachyramphus marmoratus (J.F. Gmelin, 1789), (n = 3000) afin de déterminer si les vitesses de vol d’oiseaux particulièrement rapides s’accordent avec les vitesses de croisière maximales (V_{mr}) prédites par la théorie aérodynamique. La vitesse moyenne (22.6 ± 0.21 m·s^{-1}) est significativement plus élevée que la V_{mr} prédite par quatre modèles qui utilisent des valeurs conventionnelles du coefficient de frottement parasite (C_{D_{par}}). Pour que le modèle de Penny-cuick prédise une V_{mr} de 22 m·s^{-1}, il faudrait utiliser un C_{D_{par}} de 0.05, donc inférieur à tout ce qui a été rapporté dans la littérature; pour les autres modèles, il faudrait des valeurs encore plus faibles de C_{D_{par}}. Nous concluons que la vitesse de croisière des guillemots dépasse V_{mr}. Comme les guillemots peuvent dépasser cette vitesse V_{mr} à cause de décisions comportementales, nous avons examiné deux hypothèses comportementales qui avancent que (1) c’est pour minimiser le taux de prédation et (2) que c’est pour maximiser le taux de croissance des aigrettes. Cependant, il n’y a pas de différence significative entre les vitesses de vol durant les périodes de forte (clarté) et de faible (obscurité) prédation, ni durant la période d’élevage des petits et les périodes non reproductives. Les guillemots peuvent aussi sembler voler à des vitesses supérieures à V_{mr} parce que la théorie aérodynamique sous-jacente est inexacte pour cette espèce. Afin de déterminer la fiabilité de la théorie aérodynamique chez les guillemots, nous avons comparé les fréquences de battement d’ailes (f) à celles prédites par le modèle de Penny-cuick. Le f moyen est significativement plus bas que le f_{pred} prédit par le modèle de Penny-cuick et, en général, f = 7.9 m^{-0.22} est un meilleur modèle pour les alcidés que celui de Penny-cuick. De plus, le nombre de Strouhal est particulièrement bas (0.12 ± 0.02). Les modèles aérodynamiques courants sont inadéquats pour les oiseaux à vol exceptionnellement rapide.

Introduction

Aerodynamic theories of powered flight allow for the calculation of the flight energy costs in relation to speed (Tucker 1973; Greenewalt 1975; Rayner 1979, 1993; Penny-cuick 1998). Such calculations predict a U-shaped total power curve and specify velocities where energy spent per unit time in air is minimized (V_{mr}) and energy spent per unit distance traveled is minimized (V_{ma} (Rayner 2001). Recent laboratory studies have verified that the aerodynamic power used by several species is consistent with theoretical models (Dial et al. 1997; Tobalske et al. 2003). However, there is still debate over the metabolic power needed for bird flight (Ellington 1991; Penny-cuick 1995; Alexander 1997; Rayner 2001).
1999, 2001), the variation of profile power with speed (Pennycuick 1995; Rayner 1999), and the most accurate value for the parasite drag coefficient ($C_{D_{par}}$) (Pennycuick 1995; 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).

Although there are other flight speeds that may optimize avian fitness in the long term (Norberg 1981a; Pyke 1981; Welham and Ydenberg 1988, 1993; Hedenstrom and Alestram 1995), the majority of researchers have focused on $V_{mp}$ and $V_{ur}$ because these variables do not depend on energy intake, which is a parameter that is difficult to estimate in the field. Schnell and Hellack (1979), Pennycuick (1987), and Spear and Ainley (1997) successfully predicted the flight speed of over 50 seabird species in the field based on these models. Most species flew at a speed intermediate between $V_{mp}$ and $V_{ur}$. Welham (1994) showed that birds weighing between 0.1 and 1 kg migrate at the Pennycuick model $V_{mp}$ whereas Hedenstrom and Alestram (1996) showed that Skylarks (Alauda arvensis Linnaeus, 1758) fly at $V_{mp}$ during display flight and $V_{ur}$ when migrating. However, these studies based their aerodynamic models on conventional values for $C_{D_{par}}$. Recent studies suggest a lower value for $C_{D_{par}}$ and reanalysis of the field studies with this drag coefficient shows that most birds fly well below $V_{mp}$ (Pennycuick 1997, 1998). Pennycuick (1995, 1998, 2001) cautions that aerodynamic models are only valid between $V_{mp}$ and $V_{ur}$ and that it is currently unknown if any birds flies faster than $V_{ur}$.

In this paper, we describe the flight speeds of a fast-flying auk. Marbled Murrelets, Brachyramphus marmoratus (J.F. Gmelin, 1789), are known from previous investigations to attain cruising speeds of up to 154 km h$^{-1}$ during daily commutes of up to 200 km round trip (Nelson 1997). Flight costs are high for auks in general, especially relative to other seabirds that often use gliding or flap-gliding flight. For example, Cassin’s Auklets, Ptychoramphus aleuticus (Pallas, 1811), have a high field metabolic rate for non-passerines in general (Hodum et al. 1998), whereas Thick-billed Murres, Uria lomvia (Linnaeus, 1758), feeding nestlings spend about 53% of their daily energy expenditure on flight (Gaston 1985).

Because of the high energetic cost associated with their daily commutes, it is likely that Marbled Murrelets experience strong adaptive pressure to minimize the costs of these commutes, and therefore, are good candidate species to test aerodynamic theory. Furthermore, while many seabirds reduce the cost of flight by flying in a V formation (Lissaman and Schollenberger 1970; Kshatriya and Blake 1992; Weimerskirch et al. 2001) or using the ground effect (Blake 1985; Blake et al. 1990; de la Cueva and Blake 1993), it is unlikely that Marbled Murrelets use these strategies. Marbled Murrelets rarely fly in groups of more than two and less than 5% of Marbled Murrelets observed were flying <15 wingspans from the water, which is necessary to employ the ground effect (de la Cueva and Blake 1993). Hull et al. (2001) assumed that the Pennycuick (1998) model is accurate for Marbled Murrelets to calculate the cost of nesting commutes. This was necessary because the capture-recapture techniques required for conventional energetic measurements could not be used. However, Hull et al. (2001) did not examine the robustness of Pennycuick’s model for Marbled Murrelets and their exceptionally fast flight.

At high speeds, wingbeat kinematics may change, causing some of the assumptions underlying aerodynamic flight models to fail (Rayner 1999; Combes and Daniel 2001). Pennycuick (1996, 2001) used dimensional analysis to predict the wingbeat frequencies of 47 bird species, primarily seabirds. He developed a formula that predicted the wingbeat frequency of cruising flight, $f_{ref}$. However, Pennycuick did not include a term for velocity into his dimensional calculations, and Pennycuick et al. (1996) and Tobalske et al. (2003) have shown a strong relationship between wingbeat frequency and speed. Furthermore, while changes in wingbeat frequency are often associated with changes in gait, fast-flying birds may have traded variation in gait for maintenance of speed over long periods (Rayner 1995). We compared the wingbeat frequency of wild Marbled Murrelets with Pennycuick’s $f_{ref}$ to determine if their wingbeat kinematics was consistent with relationships developed primarily from observations of slower flying species.

It is possible that fast flight may be a behavioural modification to maximize a different currency. Norberg (1981a) predicted that birds feeding nestlings would fly at speeds greater than $V_{ur}$ to maximize the rate at which food was delivered to their young. However, McLaughlin and Montgomery (1985) did not detect a significant difference in the flight speeds of female Lapland Longspurs, Calcarius lapponicus (Linnaeus, 1758), feeding nestlings compared with those incubating. Nevertheless, they suggested that there may be an energetic advantage to speeds greater than $V_{ur}$ during chick-rearing for birds that make long foraging trips. Marbled Murrelets, which carry 10–15 g fish with considerable cross-section over a long distance during chick-rearing (Nelson 1997), are therefore better candidates to test Norberg’s hypothesis. Furthermore, while other auks undergo adaptive mass loss during chick-rearing (Norberg 1981b; Croll et al. 1991), which reduces mass and therefore $V_{ur}$ obscuring the “Norberg effect”, Marbled Murrelets do not (Hull et al. 2002). Lima and Dill (1990) suggest that to maximize fitness animals will minimize the currency of predation risk per unit energy gained. As most of their predators are diurnal, Marbled Murrelets experience higher predation during the day than at night (Nelson 1997). Consequently, Marbled Murrelets may fly faster during daylight hours than after nightfall to minimize predation rate per unit energy gained.

We hypothesize that Marbled Murrelets will (i) fly at $V_{ur}$ outside of the chick-rearing period; (ii) fly faster during the chick-rearing period than other periods; (iii) fly faster during daylight than darkness; and (iv) maintain a wingbeat frequency of $f_{ref}$. In addition, we compared Marbled Murrelet flight kinematics to that of other auks to determine which trends were unique to the Marbled Murrelet and which were relevant to auks as a whole. We used egg mass relative to body mass as an indication of the mass-loading capability of Marbled Murrelets.

Tests of optimal flight speed hypotheses have been confounded by the difficulty of recording accurate field flight speeds in quantity (Blake et al. 1990; Pennycuick 1995, © 2004 NRC Canada

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Because of this, few comparisons of field flight speeds and predicted optimum speeds and wingbeat frequencies have been made, and most rely on small sample sizes (Schnell and Hellack 1979; Pye 1981; Bryant and Turner 1982; Gill 1985; McLaughlin and Montgomery 1985; Masman and Kaasen 1987; Blake et al. 1990; Evans and Drickamer 1994; Pennycuick 1997; Spear and Ainley 1997). A large sample size is important because the morphological data for individual birds is unknown in the field, and comparison of measured and predicted values is therefore statistical in nature. The use of ship-mounted radar facilitated the collection of a large number of speed measurements in a short period of time and was employed by Bruderer and Boldt (2001) to monitor flight speeds of 139 migrating species. Furthermore, few authors record kinematic data, apart from flight speed, of any kind. We recorded wingbeat amplitude and frequency, and downstroke parameter, based on digital videotapes from the field. In this paper, a large sample — the largest sample for any species ever published — of accurately recorded Marbled Murrelet flight speeds and wingbeat kinematics was statistically compared with our hypotheses.

Materials and methods

The Marbled Murrelet is a nationally threatened species in Canada largely because of its dependence on old-growth forest, and has been the focus of detailed ongoing research and monitoring in British Columbia and elsewhere in North America (Nelson 1997). Because of its conservation status and secretive nature, intrusive methods for measuring flight costs, such wind-tunnel experimentation or labeling with heavy water, are either undesirable or impractical.


The breeding chronology and breeding status of Marbled Murrelets are difficult to determine, as nests are hard to locate and access and are prone to disturbance (Hull et al. 2002). To assess changes in flight speeds in relation to breeding chronology, “core” incubation and chick-rearing periods were assigned based on Hull et al. (2001, 2002). We estimated the incubation period to be from 4 to 14 June, chick-rearing to be from 4 to 14 July, and non-breeding to be in mid-February. Very short time frames were necessary, as Marbled Murrelets have the most extended and overlapping breeding cycles of any auk (Hull et al. 2002). Only flight speeds measured at Desolation Sound were used for comparisons between different reproductive periods.

Flight speeds were measured by marking the distance between successive radar sightings (radar was set at 2 km radius) on a transparency affixed to the radar screen or a digital videotape of the radar output and averaged over at least three sightings. All measurements were confirmed visually as Marbled Murrelets. A ship-mounted radar (FURUNO model FR-8050D, 9410 ± 30 MHz) with a 1.5-m antennae mounted 5 m above the water was used to record flight speeds. Radar sweeps took 2.50 ± 0.01 s and marks were accurate within 1 mm. The major source of error was therefore in the distance measurements and the relative error decreased with flight speed. Observers using transparencies took great care to avoid errors created by parallax between the marks on the transparency attached to the monitor. Maximum error on individual ground speed measurements was 1 m s⁻¹, depending on the number of sightings used and flight speed.

Although there was no detectable wind at the boat (<1 m s⁻¹) at the time of measurement, there may have been wind at the location of the Marble Murrelets, which could be up to 2 km away. However, wind was usually in the direction of the head of the inlets, and there was no significant difference between incoming and outgoing speeds of Marbled Murrelets (Kruskal–Wallis, p > 0.6). Although the radar gives no estimate of vertical distance traveled, most Marbled Murrelets appeared to be traveling at level flight. We found no difference in outgoing versus incoming flight speeds and no support for Burger’s (1997) conjecture that outgoing birds fly faster because they have increased momentum associated with descending from the mountains.

Flight profiles of 13 Marbled Murrelets were recorded on a Sony Digital 8 DCR-TRV320 video recorder (24 frames s⁻¹) in the Desolation Sound area. Wingbeat frequency, upstroke parameter, and wing amplitudes were determined from these videotapes by slowing down the videos so that images could be viewed frame by frame. Wingbeat frequency was measured as the number of wingbeats counted divided by the duration (s) of the video footage. We estimated the upstroke parameter from the ratio of frames with the bird in upstroke to downstroke. Wing amplitude was estimated as the maximum height of the wing relative to the body over all frames in a given footage sequence.

We salvaged 10 carcasses from fisheries bycatch and other accidental mortality to measure wingspan, wing area, and cross-sectional body area. Pennycuick (1998) noted that the measurement of wing area was particularly susceptible to observer bias. Although we followed his protocol as closely as possible, the wingtip in flying Marbled Murrelets was quite broad with the primary feathers widely fanned and the ends separated. Consequently, the fully extended wing, used by Pennycuick (1998), may not reflect the effective shape of the wingtip in flight. Mass (202 ± 17 g) was estimated from 2277 birds measured in the field in the Desolation Sound area (Hull et al. 2001). Hull et al. (2002) found no change in mass over the breeding season, except for females, which lost approximately 30 g (the mass of an egg) after laying.

Statistics were calculated using JMPIn version 4.0 (SAS Institute Inc. 2000).

Aerodynamic models

Tucker (1973), Pennycuick (1975, 1998), and Rayner (1979, 1993) developed aerodynamic models for avian flapping flight. In all models, the total metabolic power P(V) required for a bird to fly is given as a function of forward velocity, V, by

\[ P(V) = R \frac{P_{\text{fl}}}{\eta} \]

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### Table 1. Names and values of parameters used in the models.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Name</th>
<th>Assigned value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$g$</td>
<td>Acceleration due to gravity</td>
<td>9.81 m·s$^{-2}$</td>
<td>Pennycuick 1998</td>
</tr>
<tr>
<td>$\rho$</td>
<td>Air density</td>
<td>1.23 kg·m$^{-3}$</td>
<td>Pennycuick 1998</td>
</tr>
<tr>
<td>$P_{mb}$</td>
<td>Basal metabolic power</td>
<td>2 W</td>
<td>Melhorn et al. 1993</td>
</tr>
<tr>
<td>$S_b$</td>
<td>Cross-sectional body area</td>
<td>0.0018±0.0001 m$^2$</td>
<td>See Methods</td>
</tr>
<tr>
<td>$k$</td>
<td>Induced power factor</td>
<td>1.2</td>
<td>Pennycuick 1998</td>
</tr>
<tr>
<td>$M$</td>
<td>Mass</td>
<td>202±3 g</td>
<td>Hull et al. 2001</td>
</tr>
<tr>
<td>$I$</td>
<td>Moment of inertia</td>
<td>0.23</td>
<td>Pennycuick 1998</td>
</tr>
<tr>
<td>$\eta$</td>
<td>Muscle efficiency</td>
<td>0.13</td>
<td>See Methods</td>
</tr>
<tr>
<td>$C_{Dpar}$</td>
<td>Parastrophic drag coefficient</td>
<td>0.02</td>
<td>Pennycuick 1998</td>
</tr>
<tr>
<td>$C_{Dpro}$</td>
<td>Profile drag coefficient</td>
<td>8.4</td>
<td>Pennycuick 1998</td>
</tr>
<tr>
<td>$\tau$</td>
<td>Downstroke:upstroke ratio</td>
<td>0.41±0.02</td>
<td>See Methods</td>
</tr>
<tr>
<td>$R$</td>
<td>Respiration factor</td>
<td>1.1</td>
<td>Pennycuick 1998</td>
</tr>
<tr>
<td>$V$</td>
<td>Velocity or speed</td>
<td>m·s$^{-1}$</td>
<td>See Methods</td>
</tr>
<tr>
<td>$S$</td>
<td>Wing area</td>
<td>0.0075±0.0006 m$^2$</td>
<td>See Methods</td>
</tr>
<tr>
<td>$f$</td>
<td>Wingbeat frequency</td>
<td>13.0±2.0 Hz</td>
<td>See Methods</td>
</tr>
<tr>
<td>$\theta$</td>
<td>Wingbeat amplitude</td>
<td>2.44±0.2</td>
<td>See Methods</td>
</tr>
<tr>
<td>$b$</td>
<td>Wingspan</td>
<td>0.44±0.01 m</td>
<td>See Methods</td>
</tr>
</tbody>
</table>

where $\eta$ is the efficiency, $R$ is the respiration factor, $P_{mb}$ is the basal metabolic power, and $P_{aer}$ is the predicted aerodynamic power that is a function of various morphometric or kinematic parameters (Table 1).

When

$$V > \frac{M}{\rho b^3 \phi} \frac{g}{f}$$

or $V > 1.3$ m·s$^{-1}$ for the Marbled Murrelet, the model developed by Rayner (1979, 1993) (i.e., Rayner’s model) predicts a continuous wake with Jones’ loading

$$P_{aer} = \frac{M^2 g^2}{4 \pi \rho b^2 V (J_0(\phi) + \cos \phi)^2}$$

$$+ \frac{1}{2} \rho V^3 (C_{Dpar} + SC_{Dpro} \delta)$$

The next three models approximate the wingbeat with an actuator disc. Although this approximation is physically unrealistic, it gives realistic power estimates that converge to the Rayner model at high speeds (Pennycuick 1995; Rayner 1999). The model described in Pennycuick (1998) (i.e., Pennycuick’s model) is the most widely used version:

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

$$+ 4^{3/4} 3^{-3/4} k^{3/4} C_{Dpar} \left( \frac{M g}{\rho V^3 S_b V^3 C_{Dpar}} \right)^{1/4}$$

A model outlined in Tucker (1973) (i.e., Tucker’s model) estimates the profile power based on the sum of induced and parasite power:

$$P_{aer} = \left( \frac{2kM^2 g^2}{\pi \rho b^2 V} + \frac{1}{2} \rho S_b C_{Dpar} V^3 \right) \left( 1 + 1.8 M^{-3/6} V^{1/2} \right)$$

A model (i.e., Aircraft model) developed directly analogous to aircraft theory has been widely used by researchers (Blake et al. 1990; Askew et al. 2001; Tobalske et al. 2003):

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

In addition, Pennycuick (1996, 2001) calculated a “benchmark” wingbeat frequency $f_{ref}$ as

$$f_{ref} = m^{3/8} g^{1/2} b^{-23/24} S^{1/3} \rho^{-3/8}$$

The calculated total aerodynamic power is plotted against flight speed in Fig. 1. Uncertainty calculations for power curves, $V_{mb}$, $V_{aer}$, and $f_{ref}$ follow the procedure described in Spedding and Pennycuick (2001).

Estimation of power curves and $V_{aer}$ is highly sensitive to the accuracy of the parameters used. We used SE to characterize the uncertainty of the mean values of kinematic and morphological data, as we were interested in statistically comparing the mean flight kinematic values with the mean values predicted by each model. We assumed no uncertainty in $g$ and $\rho$ (Pennycuick 1998).

It is difficult to characterize the uncertainty associated with aerodynamic and physiological parameters. Most researchers agree on $k = 1.2$ (Pennycuick 1998; Rayner 1999), although some authors suggest that 1.2 is a little low, and others use 1.0 (e.g., Blake et al. 1990). As can be seen in the disparity between the models, there is little agreement in the analytic form of the profile drag. Nevertheless, most authors accept a profile drag coefficient ($C_{Dpar}$) of roughly 0.02 (Pennycuick et al. 1992; Pennycuick 1998; Rayner 1999; Askew et al. 2001; Tobalske et al. 2003).

$C_{Dpar}$ is much more poorly known than $C_{Dpro}$. Data from mounted specimens ranged 0.2–0.5, depending on Reynolds’ number (Pennycuick et al. 1988). However, this system likely overestimated the drag experienced by wild birds (Tucker 1990; Pennycuick et al. 1996, 2000; Hedenstrom and Liechti 2001; Park et al. 2001). Pennycuick (1998) sug-
Fig. 1. (a) Basal metabolic power curves (W) for Marbled Murrelets, Brachyramphus marmoratus, with \( C_{D_{pr}} = 0.13 \). Note that the power curves are only valid below maximum-range speed (Pennycuick 1995). (b) Frequency histogram of flight speeds.

![Graph showing flight speeds and frequencies for different species.]

Fig. 2. Mean (±SE) flight speeds (m·s\(^{-1}\)) of Marbled Murrelets at Desolation Sound. The values are means for the week centred at each date.

![Graph showing mean flight speeds over time.]

Investigations using a value of 0.1, while Rayner (2001) suggested that both \( C_{D_{pr}} \) and \( C_{D_{pa}} \) be combined into a single coefficient with a range of 0.03–0.06; neither of which considers the effect of Reynolds’ number on \( C_{D_{pr}} \). At Reynolds’ number for Marbled Murrelets (approximately 27 000), conventional estimates of \( C_{D_{pa}} \) were about 0.4. However, Rayner (1999) suggested that the best estimate was about a third of the conventional value, giving an estimate of about 0.13. Askew et al. (2001) and Tobalske et al. (2003) used 0.13 for species with a similar Reynolds’ number to Marbled Murrelets.

The appropriate value for muscle efficiency (\( \eta \)) is also controversial. Pennycuick (1998) derived a value of 0.23 based on experiments with tilting wind tunnels. However, Ward et al. (2001) found that muscle efficiency of the European Starling (Sturnus vulgaris Linnaeus, 1758) varies with flight speed, giving a flatter than expected metabolic power curve. They suggested an average value of 0.18 for the European Starling. Although their results suggest that flight muscle efficiency may be much lower than expected in small birds, the discrepancy is likely less for larger birds (Rayner 1999), and 0.23 appears to be an adequate approximation for muscle efficiency in Marbled Murrelets, which are roughly twice the mass of European Starlings.

**Speed measurements**

The overall mean flight speed was 22.6 ± 0.1 m·s\(^{-1}\) (Fig. 1). The mean flight speed during the pre-laying period was 23.6 ± 0.7 m·s\(^{-1}\), during the incubation period was 22.4 ± 0.7 m·s\(^{-1}\), during chick-rearing was 21.2 ± 0.2 m·s\(^{-1}\), and during the non-breeding season was 21.4 ± 0.75 m·s\(^{-1}\) (Fig. 2). The only significant difference between seasonal flight speeds was during the pre-laying period (Kruskal–Wallis, \( p < 0.05 \)), which was likely because female Marbled Murrelets weighed 30 g more during this period as they were carrying eggs (Hull et al. 2002).

The models predicted a \( V_{mr} \) between 12 and 27 m·s\(^{-1}\), depending on \( C_{D_{pr}} \) (Table 2). The \( V_{mr} \) for the Aircraft and Rayner models was significantly different from the measured mean flight speed, even with a \( C_{D_{pa}} \) of 0.03 (Kruskal–Wallis, \( p < 0.05 \)). However, the calculated \( V_{mr} \) for the Pennycuick and Tucker models was not significantly different from the mean speed (22.6 m·s\(^{-1}\)) with a \( C_{D_{pa}} \) of 0.06 and 0.05, respectively. All models were significantly different (Kruskal–Wallis, \( p < 0.05 \)) from the mean measured flight speeds with the \( C_{D_{pa}} \) estimate of 0.13 suggested above; Rayner’s suggestion of 0.03–0.06 provided a better fit.

The mean wingbeat frequency of 12.9 ± 0.5 s\(^{-1}\) (Fig. 3) did not vary significantly between the non-breeding and breeding seasons but was significantly different from the value of \( f_{ref} \) derived from the Pennycuick model.

**Discussion**

The mean measured speeds were statistically greater than \( V_{mr} \) for all four models with realistic values of \( C_{D_{pa}} \). Although other seabirds fly faster near their colony than their mean commute velocity (Bvenenuti et al. 1998), as we found no variation in flight speeds relative to our position in coastal inlets or direction of flight, we believe that our results represent mean commute speeds of Marbled Murrelets. We conclude that either the models are incorrect or Marbled Murrelets exceed \( V_{mr} \).

Flight models that incorporate wingtip shape (Combes and Daniel 2001; Lockwood et al. 1998) and unsteady aerodynamics (Sunada and Ellington 2001; Rayner 1999) may be necessary to fully understand avian flight. However, as most auk flight speeds coincided with the \( V_{mr} \) predicted by conventional models (Pennycuick 1987), varied approximately by \( M^{0.56} \) (Fig. 4) as expected (Pennycuick 1987), and there was nothing obviously unusual about Marbled Murrelet wingbeat kinematics or wing shape, we believe that these models likely accurately describe Marbled Murrelet aerodynamics. In particular, while most birds have a Strouhal num-

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Table 2. Maximum-range speeds (m·s⁻¹) for the Marbled Murrelet, Brachyramphus marmoratus, predicted by each model with different values of parasite drag coefficients (C_{D_{par}}).

<table>
<thead>
<tr>
<th>Aerodynamic model</th>
<th>Values of C_{D_{par}}</th>
<th>0.40</th>
<th>0.20</th>
<th>0.10</th>
<th>0.05</th>
<th>0.03</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rayner</td>
<td>12.7±1.4</td>
<td>14.9±1.5</td>
<td>16.7±1.5</td>
<td>18.8±1.6</td>
<td>20.1±1.6</td>
<td></td>
</tr>
<tr>
<td>Pennyucick</td>
<td>14.2±1.2</td>
<td>16.9±1.2</td>
<td>19.7±1.2</td>
<td>23.4±1.2</td>
<td>26.6±1.2</td>
<td></td>
</tr>
<tr>
<td>Tucker</td>
<td>13.8±1.2</td>
<td>16.4±1.2</td>
<td>19.2±1.2</td>
<td>22.7±1.2</td>
<td>25.8±1.3</td>
<td></td>
</tr>
<tr>
<td>Aircraft</td>
<td>12.6±1.2</td>
<td>14.5±1.2</td>
<td>15.8±1.2</td>
<td>17.1±1.2</td>
<td>17.8±1.2</td>
<td></td>
</tr>
</tbody>
</table>

Note: Error calculated according to Spedding and Pennyucick (2001).

Fig. 3. Frequency distribution of wingbeat frequencies of Marbled Murrelets (n = 32).

Fig. 4. Flight speeds (V; m·s⁻¹) of auks and diving-petrels as a function of mass (M; g). Linear regression of log–log plot without the Marbled Murrelet datum (●) gives V = 19.05M^0.12 and R² = 0.88. Data, except the Marbled Murrelet datum, are from Pennyucick (1987).

ber between 0.2 and 0.3 (Taylor et al. 2003), the Strouhal number for Marbled Murrelets is f/D_{wing} = 0.12 ± 0.02, suggesting that there are no unsteady aerodynamics.

These models may accurately estimate aerodynamic power, but incorrectly estimate metabolic power. Although laboratory studies have validated the aerodynamic power curve models (Dial et al. 1997; Tobalske et al. 2003), these models have not been successful at predicting the total metabolic power as a function of flight speed in the laboratory. Many species appear to have a rather flat metabolic power curve, likely the result of variable flight muscle efficiency, which implies that a large speed range could be exploited at a similar cost (Ellington 1991; Alexander 1997; Rayner 1999; Ward et al. 2001; Kvist et al. 2001). A flat power curve would explain why Marbled Murrelets did not change their speed in response to predation or chick-rearing, as these models are only valid for species with U- or J-shaped power curves (Norberg 1981a; Lima and Dill 1990).

Although we found no evidence that Marbled Murrelets optimize any particular energetic currency (nestling energy intake, energy gain per predation rate, or V_{mr}), there are other speeds that may optimize avian fitness (Pyke 1981; Welham and Ydenberg 1988, 1993; Hedenstrom and Alerstam 1996). Future investigations could address these currencies by quantifying prey abundance of Marbled Murrelets.

At high flight speeds, increasing the thrust to accommodate additional mass (i.e., egg, food) represents a proportionately small increase to the total cost of flight (Rayner 1999), and there is little extra cost in climbing to high elevations. For example, many fast-flying auks, such as Marbled Murrelets, nest higher than slower flying ones (Gaston and Jones 1998; Hull et al. 2001), and auks have relatively larger eggs than the slower flying petrels (Rahn et al. 1984; Fig. 5). Because of the high cost of flapping flight, Marbled Murrelets and other auks spend less than 2 months breeding and typically fledge chicks at 60% of adult size (Ydenberg 1989; Gaston and Jones 1998). The cost of added mass (i.e., here represented by egg mass, food load, and altitude gain) may be mitigated by variable efficiency (Rayner 1999; Kvist et al. 2001), and Marbled Murrelets may have evolved high flight muscle efficiency over a wide range of speeds as a strategy to overcome the high cost of chick-rearing, allowing them to fly exceptionally fast.

The failure of aerodynamic models to predict the mean flight speed of Marbled Murrelets highlights the models' limitations and the need for caution when using them to calculate energy expenditure, as done by Hull et al. (2001), Pennyucick (1995, 1998) noted that since wind-tunnel experiments have only used speeds below V_{mr}, energy estimates above V_{mr} were uncertain, and based on our results, inaccurate for the Marbled Murrelet. Estimates of V_{mr} are difficult in general owing to the models' sensitivity to k, C_{D_{par}}, C_{D_{par}}/\eta (Pennyucick 1995, 1997, 1998; Rayner 1999, 2001), and S (Schnell and Hellback 1979; Pennyucick 1995, 1998). Early work on flight speed suggested that most birds flew between V_{mr} and V_{mr} (Schnell and Hellack 1979; Pennyucick 1987; Welham 1994; Hedenstrom and Alerstam 1996; Spear and Ainley 1997); however, revision with more recent values for C_{D_{par}} suggested that most birds fly substantially below V_{mr} (Pennyucick 1997, 1998). Thus, the Marbled Murrelet is an exceptionally fast flyer. The large speed range used by Marbled Murrelets suggests that caution is needed before using speed to identify this species by radar as recommended by Burger (1997, 2001).

Wingbeat frequencies of Marble Murrelets are significantly less than predicted (Pennyucick 1996). Using a nonlinear least-squares regression (eq. 3, constraints 4–6 in
Table 3. Morphological data and wingbeat frequencies (f) for auks and diving petrels.

<table>
<thead>
<tr>
<th>Species</th>
<th>Observed values</th>
<th>Calculated values</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M (kg)</td>
<td>S (m²)</td>
</tr>
<tr>
<td>Razorbill, Alca torda Linnaeus, 1758⁹</td>
<td>0.62</td>
<td>0.0462</td>
</tr>
<tr>
<td>Common Murre, Uria aalge (Pontoppidan, 1763)⁹</td>
<td>0.95</td>
<td>0.0544</td>
</tr>
<tr>
<td>Pigeon Guillemot, Cepphus columba Pallas, 1811</td>
<td>0.45</td>
<td>0.0179</td>
</tr>
<tr>
<td>Marbled Murrelet, Brachyramphus marmoratus</td>
<td>0.21</td>
<td>0.008</td>
</tr>
<tr>
<td>Ancient Murrelet, Synthliboramphus antiquus (J.F. Gmelin, 1789)</td>
<td>0.21</td>
<td>0.008</td>
</tr>
<tr>
<td>Rhinoceros Auklet, Cerorhinca monocerata (Pallas, 1811)</td>
<td>0.45</td>
<td>0.0168</td>
</tr>
<tr>
<td>Atlantic Puffin, Fratercula arctica (Linnaeus, 1758)⁹</td>
<td>0.4</td>
<td>0.0369</td>
</tr>
<tr>
<td>Tufted Puffin, Fratercula cirrhata (Pallas, 1769)</td>
<td>0.79</td>
<td>0.062</td>
</tr>
<tr>
<td>Common Diving Petrel, Pelecanoides georgicus Murphy and Harper, 1916⁹</td>
<td>0.11</td>
<td>0.0197</td>
</tr>
<tr>
<td>South Georgia Diving Petrel, Pelecanoides urinatrix (J.F. Gmelin, 1789)⁹</td>
<td>0.13</td>
<td>0.0221</td>
</tr>
</tbody>
</table>

Note: Values not marked with a footnote are products of the current study.
⁸Gaston and Jones 1998.
⁷Hull et al. 2001.
⁶Pennycuick 1996.

Fig. 5. Egg masses relative to wing loadings for various seabirds.

Fig. 6. Wingbeat frequencies (Hz) of auks as a function of mass (g) and wingspan (m). Linear regressions are log(wingbeat frequency) = −0.59log(wingbeat frequency) + 0.86 and log(wingbeat frequency) = −0.19log(mass) + 0.93.

Pennycuick (1996), we derived $f_{ref} = 7.9m^{-1/6}$ as a best fit for auks and structurally similar diving petrels (Pelecanoides spp.) (Fig. 6, Table 3), which is consistent with predictions by Pennycuick (1975) based on avian muscle mechanics. Variation in $b$ and $S$ was not significantly different from zero, suggesting that for the auks constraints on muscle performance may be more important than variation in wingbeat cinematics. The new equation ($R^2 = 0.80$) is better than Pennycuick’s at predicting wingbeat frequencies. The actual value of our exponent (−0.22) is somewhat lower than −1/6 and closer to −0.33, which is the value for maximal power during takeoff (Askew et al. 2001), suggesting that cruising flight in auks may be close to their maximal power limitations.

Van den berg and Rayner (1995) noted that the wingspan exponent in the expression for the moment of inertia ($I$) was larger than expected for diving birds and suggested that this may be why the usual relationship $f \propto b^{-1}$ did not hold for these species. In our data, $f \propto b^{-2}$ with $R^2 = 0.74$ (Table 3, Fig. 6). As Pennycuick’s derivation assumed $f \propto mb^2$, this may explain why his relationships did not hold for the auks.

Like Pennycuick (1996), our calculations assume that $f$ is independent of $V$. As $f$ is roughly correlated with power, (Pennycuick et al. 1996; Dial et al. 1997; Park et al. 2001; Tobalske et al. 2003) this would suggest a J-shaped power curve for auks. Mordvinov’s (1992) and Meinerzhagen’s (1955) $f$ for Common Murre and Pigeon Guillemot are much lower than either our own values or those of Pennycuick (1996). However, their measurements were done by counting wingbeats in the field, a method unreliable at the high fre-
quencies characteristic of auks, or near the colony where $f$
decreases because auks may use "butterfly flight" (Gaston and
Jones 1998).

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