

## S36-1 The flight energetics of barnacle geese (*Branta leucopsis*) under wild and captive conditions

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**Abstract** Experimental data on the relationship between mean heart rate ( $f_H$ ) and mean rate of oxygen consumption ( $VO_2$ ) of captive barnacle geese during flights in a wind tunnel are reviewed in terms of their capacity to predict the mean  $VO_2$  of wild barnacle geese, based on recordings of their  $f_H$  during autumn migratory flights between Spitsbergen (78°N) and Scotland (55°N).  $f_H$  increased linearly with simultaneously recorded  $VO_2$  in a single barnacle goose flying in the wind tunnel ( $VO_2 = 1.42 f_H - 304$ ,  $r^2 = 0.82$ ,  $P < 0.001$ ,  $N = 12$  flights). The mean  $f_H$  of wild migratory barnacle geese was 253 beats  $min^{-1}$ . Substitution of this value into the above calibration equation results in an unrealistically low value for mean migratory  $VO_2$  of only 55  $ml\ min^{-1}$ . Factors such as difference in heart mass, selective tissue perfusion, environmental temperature and formation flight may account for some of the difference in  $f_H$  between the captive and wild geese.

**Key words** Migration, Energetics, Geese, Heart rate, Oxygen consumption, *Branta leucopsis*

### 1 Introduction

It is not easy to obtain cardiovascular, respiratory and energetic data from animals during flight, either under captive or wild conditions; and very few techniques are applicable to both situations. No single approach can adequately give all of the necessary information required for a full analysis of the physiological responses to flight. The respiratory and cardiovascular systems of birds and mammals are primarily designed to enable gas exchange and molecular flux between the circulating blood supply and various organs and tissues and the external environment (Schmidt-Nielsen, 1997). This process is especially demanding during sustained locomotor activities, in order to support the prolonged metabolic activity of the muscles by continuously oxidizing stored fuels to yield high energy bonds within molecules of ATP. The rate at which oxygen is taken up by the lungs and delivered to the working muscles is closely correlated with the rate of circulation of blood (and hence, oxygen) around the body, and with its eventual utilization in oxidative phosphorylation (Weibel et al., 1991). Thus, the rate of oxygen consumption ( $VO_2$ ) gives an indication of the rate of fuel oxidation required to sustain locomotor activity and associated aerobic physiological processes.

Recent technological advances have enabled the development of biotelemetry and data logging devices which have been successfully deployed in studies of the physiology and behavior of free-flying birds (Butler and Woakes, 1980; Butler et al., 1998; Weimerskirch et al., 2000). For

running, swimming and gliding, in particular, it has been demonstrated that, when properly calibrated and when mean data are used from a number of individuals, heart rate ( $f_H$ ) can be measured and used as an indicator of  $VO_2$  in free-living birds (Nolet et al., 1992; Bevan et al., 1994, 1995a,b; Green et al., 2001). However, the relationships between  $f_H$  and  $VO_2$  during resting, walking and running, or during swimming, may not necessarily be the same as when the birds are flying (Gessaman, 1980; Nolet et al., 1992; Butler et al., 2000). In general, it is recommended that, where possible, the range of  $f_H$  values recorded in the field should not exceed the range of  $f_H$  measured during calibration. Thus,  $f_H$  should be calibrated against  $VO_2$  for birds during flapping flight before the method can be used reliably to determine the  $VO_2$  of free-flying birds in the wild, as  $f_H$  during flight can be much greater than that during hind limb exercise (Nolet et al., 1992; Butler et al., 1998; Butler et al., 2000).

The general relationship between  $f_H$  and  $VO_2$  is described by the Fick equation

$$VO_2 = f_H \times V_s \times (C_a O_2 - C_v O_2) \quad (1)$$

where  $V_s$  is cardiac stroke volume,  $C_a O_2$  the oxygen content of arterial blood, and  $C_v O_2$  the oxygen content of mixed venous blood. This relationship can be used as a basis to model predictions for the  $VO_2$  of birds during forward flapping flight (Bishop and Butler, 1999; Bishop, 1997, 1999), or used in conjunction with data obtained from calibration studies.

The increased use of wind tunnels over the past few decades has greatly increased our understanding of the

physiology, biomechanics and aerodynamics of birds during gliding and flapping flight (Butler et al., 1977; Butler and Woakes, 1990; Norberg, 1990; Pennycuick et al., 1996; Dial et al., 1997; Kvist et al., 1998; Rosén and Hedenström, 2001). The wind tunnel itself may influence bird behavior and wing kinematics during flight, so it is important where possible to compare these data with those from free-flying birds (Butler et al., 1977; Rayner, 1994). Given such potentially direct effects from experimental conditions, and the indirect effects of captive husbandry on attributes such as physical fitness, it would be valuable to compare data collected from animals living in the wild with that from animals in captivity. In this paper we will review the experimental data on the relationship between mean heart rate ( $f_H$ ) and mean  $VO_2$  of captive barnacle geese during flights in a wind tunnel (Ward et al., 2002), in terms of their capacity to predict the typical  $VO_2$  of wild barnacle geese, based on recordings of their  $f_H$  on autumn migratory flights between Spitsbergen (78°N) and Caerlaverock, Scotland (55°N) (Butler et al., 1998).

## 2 $F_H$ and $VO_2$ of captive barnacle geese flying in a wind tunnel

Ward et al. (2002) trained young barnacle geese (1.6 to 2.3 kg) to fly in a large wind tunnel, and to walk on a treadmill while covered by a respirometry chamber. They simultaneously measured the  $VO_2$  and  $f_H$  of 5 individuals on the treadmill ( $N=50$ ) and 4 individuals in the wind tunnel ( $N=15$ ), although in the latter case one bird made almost all the flights ( $N=12$ ). A full description of the wind tunnel is provided in Ward et al. (2002). Following 6 weeks of training, heart rate data loggers which stored  $f_H$  as averages over 30 s intervals (Woakes et al., 1995) were implanted into the abdomens of the geese under sterile conditions (Butler et al., 2000). The birds were given one week to recover before a further 3 weeks of experimental flights (Ward et al., 2002). In order to measure the rate of oxygen consumption and heart rate during flight, geese were flown wearing a lightweight, clear polyurethane mask (4.4 g) which covered the beak and nares. Data where both  $f_H$  (beats  $min^{-1}$ ) and  $VO_2$  (ml  $min^{-1}$ ) were recorded simultaneously are presented in Fig. 1, but only the data from goose B-B are used to calculate the regression relationship between  $f_H$  and  $VO_2$ . Data are presented as the overall mean values recorded over complete flights ( $N=12$  flights).

Ward et al. (2002) show (Fig. 1) that the linear regression equation for 5 barnacle geese walking/running on a treadmill (i.e. terrestrial locomotion) was

$$VO_2 = 0.32f_H - 11, r^2 = 0.70 \quad (2)$$

while that for goose B-B flying in a wind tunnel was

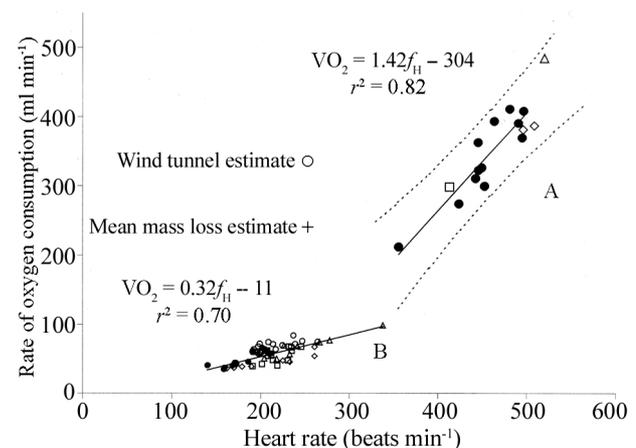
$$VO_2 = 1.42f_H - 304, r^2 = 0.82 \quad (3)$$

The slopes and intercepts of the relationship for the calibration of  $f_H$  and  $VO_2$  during flight are significantly different from those during terrestrial locomotion (ANCOVA: intercept  $F_{1,22} = 9.2, P = 0.007$ ; slope  $F_{1,22} = 7.9, P = 0.01$ ).

## 3 Heart rate from other studies of wild and captive barnacle geese

The values for  $f_H$  measured in other experiments and observations of captive and wild barnacle geese during flight in a wind generator or during free-ranging flights are shown in Fig 2. Using data loggers, Butler et al. (1998) measured the  $f_H$  of four geese flying on autumn migration between Spitsbergen and Scotland. Mean  $f_H$  at the beginning of the flight from Spitsbergen was  $317 \pm 9$  beats  $min^{-1}$ . As it progressed, mean  $f_H$  gradually declined until it reached a low point of  $226 \pm 10$  beats  $min^{-1}$ , after approximately 70% of the mean total journey time had elapsed ( $61.3 \pm 2.5$  h; Butler et al., 1998). Mean  $f_H$  for the entire migratory flight was  $253 \pm 10$  beats  $min^{-1}$ . The values for  $f_H$  from the wild geese are substantially lower than the mean values of  $512 \pm 4$  beats  $min^{-1}$  for geese (body mass  $M_b = 1.7$  kg) trained to fly behind a truck (Butler and Woakes, 1980) and  $378 \pm 15$  beats  $min^{-1}$  for geese ( $M_b = 1.7$  kg) trained to fly in front of a wind generator (WG) in Toronto (Butler et al., 2000). A mean value for  $f_H$  of  $451 \pm 23$  beats  $min^{-1}$  ( $N=4$  birds) was recorded in barnacle geese flying unencumbered by respirometry masks in the Birmingham wind tunnel (WT; Ward et al., 2002). In the latter study,  $f_H$  was measured from birds flying at a distance of more than 1 m away from the trainer, where the trainer had no detectable effect on  $f_H$ .

## 4 Discussion



**Fig. 1** Linear regression relationships between mean heart rate ( $f_H$ , beats  $min^{-1}$ ) plotted against mean rate of oxygen uptake ( $VO_2$ , ml  $min^{-1}$ ) of barnacle geese flying in a wind tunnel (A) and walking on a treadmill (B)

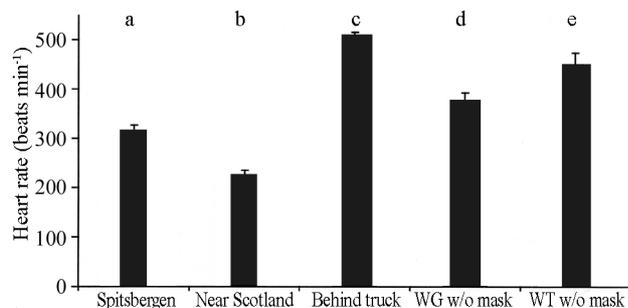
The filled dots represent mean values for individual exercise bouts for one barnacle goose (B-B), from which most data on the relationship between  $f_H$  and  $VO_2$  during flight were obtained ( $N=12$  flights). The open symbols represent mean values from 3 additional birds during flight ( $N=4$ ) and 4 additional birds during walking ( $N=50$ ). The dotted lines = 95% prediction intervals for goose B-B during flight. Data from Ward et al. (2002). Also presented are estimates for mean  $VO_2$  of wild migrating geese based on wind tunnel data (large open circle) and minimum mass loss data (large cross) plotted against mean  $f_H$  during migration.

#### 4.1 Calibration of $f_H$ and $VO_2$ during walking and flight in captive barnacle geese

Nolet et al. (1992) suggested that the  $f_H/VO_2$  relationship in barnacle geese during terrestrial locomotion could not be the same as that during flight. This suggestion is clearly confirmed by the results presented in Fig. 1, where the extrapolation of regression equation (2) for running geese does not predict realistic values of  $VO_2$  from the values of  $f_H$  recorded for flying geese, and vice versa. At an  $f_H$  of around 350 beats  $min^{-1}$ , the  $VO_2$  of the flying geese is approximately twice as great as that during running, and this is likely to result from both a relative increase in cardiac stroke volume and so cardiac output (Bishop and Butler, 1995), and an associated increase in oxygen extraction from the blood (Butler et al., 1977). This might be expected because barnacle geese have flight muscles that are approximately twice as large as the total musculature of the legs (Bishop et al., 1996) and, in addition, a higher aerobic capacity (Bishop et al., 1995).

#### 4.2 Predictions of $VO_2$ in wild migrant barnacle geese

*Using the  $f_H$  and  $VO_2$  calibration of captive birds flying in the wind tunnel* In principle, it should be possible to use the calibration relationship for  $f_H/VO_2$  during flight in the wind tunnel to estimate  $VO_2$  in wild migrant flying barnacle geese, based on recordings of  $f_H$  made using data loggers during migration (Butler et al., 1998). However, the ability to predict mean  $VO_2$  in wild migrating geese from the calibration of  $f_H$  in the wind tunnel is based on the assumption that the captive-bred birds do not differ from wild birds in wing morphology, in the physiology and morphology of the heart and the major locomotory muscles, nor in the major constituents of the blood. An additional assumption is that there is no large difference in physiological and environmental variables, such as air temperature, that might influence the peripheral resistance of the blood vasculature. Large changes in any of these variables could alter the relationship between  $f_H$ , stroke volume and oxygen extraction,



**Fig. 2** Mean  $f_H \pm SE$  recorded from wild barnacle geese (a) flying at start of autumn migration from Spitsbergen and (b) flying on approach to Scotland, and from captive barnacle geese (c) flying behind a truck, (d) flying without respirometry mask in front of a wind generator (WG), and (e) flying without respirometry mask in a wind tunnel (WT) Data from Butler and Woakes (1980), Butler et al. (1998), Butler et al. (2000) and Ward et al. (2002).

and hence that between  $VO_2$  and  $f_H$ .

Fig. 2 shows that the mean  $f_H$  of captive geese flying in the wind tunnel was generally much higher than that of migrating wild geese. Thus, when using the mean  $f_H$  recorded during migratory flights in equation (3), the prediction of  $VO_2$  in wild, migrating geese is unrealistically low (55  $ml\ min^{-1}$ ). Therefore, the  $f_H/VO_2$  relationship for captive geese during flight must be different from that in wild migratory geese (Butler et al., 1998). This suggests that a number of the assumptions mentioned above are not fulfilled.

*Using the  $VO_2$  of captive birds flying in the wind tunnel* Taking the value of  $f_H$  (451 beats  $min^{-1}$ ) obtained for captive barnacle geese during flights in the wind tunnel without a respiratory mask (Fig. 2), we can use regression equation (3) to predict the  $VO_2$  of captive birds in unencumbered flight (Ward et al., 2002). Equation (3) yields a prediction for  $VO_2$  for geese flying in the wind tunnel of  $336 \pm 31\ ml\ min^{-1}$  (mean body mass 2.06 kg,  $N = 4$ ). This gives a mass-specific value of  $163\ ml\ min^{-1}\ kg^{-1}$ . Over the range of speeds (16–19  $m\ s^{-1}$ ) that barnacle geese were usually prepared to fly for 6–10 minutes in the wind tunnel, there was no significant effect of flight speed on  $VO_2$  (Ward et al., 2002). Therefore, the above estimate of  $VO_2$  probably represents the minimum power required for forward flapping flight in the wind tunnel.

This estimate for minimum  $VO_2$  during flight in a wind tunnel should reasonably be considered to be a slight overestimate for the minimum power required by barnacle geese during free-ranging flight. Although the  $f_H$  of the birds in the wind tunnel was recorded during unencumbered flight and without help from a respiratory mask and trainer, any relatively unstable posture (e.g., head turning), turbulence in the wind tunnel and stress associated with the laboratory environment, would all tend to increase flight costs. In addition, the primary feathers had become abraded by aviary conditions.

*Mass loss estimates* During field studies conducted by Bishop et al. (1996), four birds were caught in Hornsund, southern Spitsbergen, towards the end of the premigratory period. Average body mass was  $2.302 \pm 0.099\ kg$  compared to an average of 1.746 kg for 13 geese caught in Scotland on 4th October (Owen and Ogilvie, 1979). Assuming no evolutionary shift in the mean size during this period, these data give a mean body mass difference of 556 g between pre- and post-migratory geese. This figure represents our best estimate for minimum body mass loss in barnacle geese performing the complete migration of around 2 500 km between Hornsund and Scotland. Total flying time for this migration is, on average, 61 h. (Butler et al., 1998). Assuming that the metabolic energy consumed during the migration comes from 96% lipid stores and 4% from proteinaceous tissue (Le Maho et al., 1988; Butler et al., 1998), the average  $VO_2$  required to metabolize 556 g of body tissue during 61 h of flight is  $241\ ml\ min^{-1}$ .

This estimate for minimum mean mass loss during

migratory flight should reasonably be considered a slight underestimate, as the birds caught in Hornsund were still premigratory, and it is possible that they could have had at least another week to continue gaining weight before migration. The mean difference in body mass between premigratory geese in Hornsund and post-molting adult geese caught earlier in the season at their normal breeding site in Spitsbergen ( $1.825 \pm 0.057$ ) can be accounted for by an average body mass increase of 24 g per day (Bishop et al., 1996). Thus, an extra week of premigratory feeding could theoretically have resulted in an average body mass difference of up to 723 g between pre- and post-migration. Moreover, some birds require as little as 5 days to complete the migration between Spitsbergen and Scotland, while others take 2 or 3 weeks (Butler et al., 1998). One possible explanation for this is that only the fattest birds are in sufficiently good condition to fly for around 61 h in the space of 5 days, as there would be little chance for significant refueling during that time. If geese do take opportunities to take on additional fuel, then this yields a final prediction for the maximal body mass change over a migration period of 5 days of up to 783 g. The average  $\text{VO}_2$  required to metabolize 783 g of body tissue during 61 h of flight is  $339 \text{ ml min}^{-1}$ . This figure is very similar to the predicted value for unrestrained flight in the wind tunnel ( $336 \pm 31 \text{ ml min}^{-1}$ ), which we have argued above is probably a slight overestimate of the cost of flight for free-flying wild birds.

As stated, we would expect the energetic cost of flight for captive and wild barnacle geese of a given morphology and body mass to be similar. Thus, we will use the above wind tunnel value ( $336 \text{ ml min}^{-1}$ ;  $M_b = 2.06 \text{ kg}$ ) as an upper estimate, and the minimum mass loss value ( $241 \text{ ml min}^{-1}$ ) as a lower estimate, for the mean costs of migratory flight between Spitsbergen and Scotland. The four wild premigratory geese had an average  $M_b$  of 2.3 kg so, assuming no extra increase in mass, this would give an approximate mean body mass for the migratory flight of around 2 kg, similar to the mean mass in wind tunnel birds. These estimates for mean migratory  $\text{VO}_2$  and body mass can then be associated directly with the measured mean value for the migratory  $f_H$  ( $253 \text{ beats min}^{-1}$ ) recorded from four barnacle geese during autumn migration (Butler et al., 1988).

Fig. 1 shows these predictions for the maximum and minimum mean  $\text{VO}_2$ s in wild migrant barnacle geese, calculated respectively from  $f_H$  in the wind tunnel and field data for mass loss, plotted against the mean value for  $f_H$  during migration, and alongside the power equation calibrating  $f_H$  and  $\text{VO}_2$  for the captive geese flying in the wind tunnel. If wild and captive geese were physiologically and morphologically similar, and flew in similar environmental conditions, it would be expected that the values for the predicted maximum and minimum mean migratory  $\text{VO}_2$ s for wild barnacle geese would lie close to the  $f_H/\text{VO}_2$  calibration line. As this is not the case, then some or all of these conditions or assumptions must differ between the two populations.

### 4.3 Modeling the cardiovascular responses of captive

### and wild migrant geese

The heart mass ( $M_h$ ) of wild premigratory barnacle geese (22.1 g; Bishop et al., 1998) was 30% greater than that of captive geese (17 g) flying in the wind tunnel (unpublished data). Bishop and Butler (1995) and Bishop (1997) used the Fick relationship in equation (1) to model predictions for the  $\text{VO}_2$  of birds during forward flapping flight. Bishop (1997) showed that for mammals, maximum sustainable cardiac output ( $V_b$ ) was a function of heart mass, and calculated that

$$V_b = 212.7 M_h^{0.879 \pm 0.036} \quad (4)$$

The highest sustained mean  $f_H$  recorded during a single flight by a captive barnacle goose was  $520 \text{ beats min}^{-1}$ . Thus, assuming that cardiac muscle in birds has a similar physiological and biomechanical performance to that in mammals (Bishop, 1997), equation (4) predicts that for a captive barnacle goose, maximum cardiac stroke volume ( $V_s$ ) = 4.96 ml. If the maximum  $f_H$  of wild geese is similar to that of captive geese, then the predicted  $V_s$  for wild migrants is 6.24 ml.

Grubb (1983) showed that the  $V_s$  of birds at rest ( $V_{s,\text{rest}}$ ) scaled as

$$V_{s,\text{rest}} = 0.18 M_h^{1.05} \quad (5)$$

This would suggest a  $V_{s,\text{rest}}$  for the captive barnacle geese of 3.53 ml, compared with the estimate for  $V_s$  during flight ( $V_{s,\text{flight}}$ ) of 4.96 ml from equation (4). The prediction that  $V_{s,\text{flight}}$  may be larger than  $V_{s,\text{rest}}$  by 1.4 fold is consistent with the results of Bishop and Butler (1995), who reanalysed data from the study of Butler et al. (1977) and suggested that  $V_{s,\text{flight}}$  of pigeons could be approximately 1.4-fold greater than  $V_{s,\text{rest}}$ . If a similar increase in  $V_s$  also occurred in barnacle geese during flight, this would contribute to the difference in the relationship between the  $f_H/\text{VO}_2$  in walking and flying geese (Fig. 1; Nolet et al., 1992; Butler et al., 2000). In addition, the greater cardiac output could be associated with a larger value for oxygen extraction (see below), so there would be a further increase in  $\text{VO}_2$  for a given value of  $f_H$  when flying.

We can investigate and visualize the possible effect of an increase in  $V_s$  between flying and walking, and a further increase in  $V_{s,\text{flight}}$  between wild migrating geese and their captive counterparts due to their larger hearts, by estimating values for cardiac output ( $V_b$ ) and plotting them against the measured values of  $\text{VO}_2$ . Fig. 3 plots the estimated relationship between the  $V_b$  and  $\text{VO}_2$  of walking and flying captive barnacle geese, calculated by multiplying the measured values for  $f_H$  during walking by the estimated  $V_{s,\text{rest}}$  using equation (5), and multiplying the values for  $f_H$  during flying by the estimated  $V_{s,\text{flight}}$  using equation (4). The linear regression for the estimated relationship between  $V_b$  and  $\text{VO}_2$  during flight then is

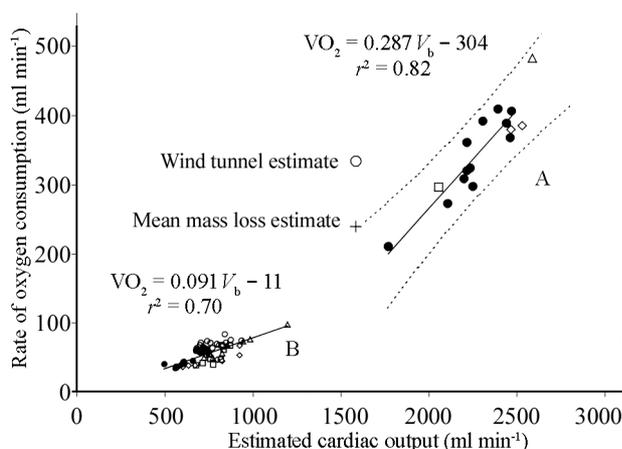
$$\text{VO}_2 = 0.287 V_b - 304.4, \quad r^2 = 0.82 \quad (6)$$

In theory, we would expect equations (4) and (5), which are based on an allometric function of  $M_h$ , to be ap-

plicable to wild and captive birds and, therefore, that equation (6) would also be similar for both captive and wild barnacle geese if heart mass alone varied between the two groups. Thus, using the measured value for mean  $f_H$  from the wild, migrating geese, we can estimate their  $V_b$ , using the  $V_{s,flight}$  of 6.24 ml based on their heart mass. The estimate for  $V_b$  in the wild geese is plotted in Fig 3 against the maximum and minimum mean  $VO_2$ , calculated from  $f_H$  in the wind tunnel and field data on mass loss, respectively. The higher estimate for minimum  $VO_2$  in the migrants is well above the calibration line for captive birds, while the minimum estimate of  $VO_2$  lies close to the 95% prediction interval of the data for wind tunnel birds. It is clear from Fig. 3 that, while the larger hearts of the wild geese will have a major impact on the relationship between  $f_H$  and  $VO_2$ , our current data cannot account for all of the apparent differences between wild and captive geese.

#### 4.4 Additional factors affecting the $f_H/VO_2$ relationship of geese during flight

There are various confounding variables that could be taken into account. Any possible reduction of peripheral circulation experienced during flight, or selective vasoconstriction to other tissues, would tend to divert blood towards the working muscles (Butler et al., 1988; Bevan and Butler, 1992) and could also increase oxygen extraction for a given value of  $f_H$  and  $V_b$ , thus shifting the  $f_H/VO_2$  and  $V_b/VO_2$  curves further to the left. Selective perfusion of tissues



**Fig. 3** Linear regression relationships between estimated mean cardiac output ( $V_b$ ,  $\text{ml min}^{-1}$ ) plotted against mean rate of oxygen consumption ( $VO_2$ ,  $\text{ml min}^{-1}$ ) of barnacle geese flying in a wind tunnel (A) and walking on a treadmill (B). The filled dots represent mean values for individual exercise bouts for one barnacle goose (B–B), from which most data on the relationship between  $f_H$  and  $VO_2$  during flight were obtained ( $N = 12$  flights). The open symbols represent mean values from 3 additional birds during flight ( $N = 4$ ) and 4 additional birds during walking ( $N = 50$ ). The dotted lines = 95% prediction intervals for B–B during flight. Also presented are estimates for mean  $VO_2$  of wild migrating geese based on wind tunnel data (large open circle) and minimum mass loss data (large cross) plotted against estimated mean  $V_b$  during migration.

vital for support of flight could possibly occur in wild migrants as a physiological strategy to maximize flight performance, and account for much of the remaining difference between  $f_H$  recorded in the wild and in the wind tunnel. The barnacle geese flying in the wind tunnel experienced higher air temperatures than those in the Arctic and may have been relatively heat stressed, leading to a potential increase in blood flow to the legs and feet and a consequent reduction in overall oxygen extraction for a given value of  $f_H$  and  $V_b$ .

It has also been suggested that migrant birds such as geese may gain significant aerodynamic advantage by flying in flock formation (Lissaman and Shollenberger, 1970; Hummel, 1995). In theory, the consequent effect of reducing both the  $f_H$  and  $VO_2$  of geese flying in formation could be considerable. Weimerskirch et al. (2001) have shown that pelicans when flying in formation have values of  $f_H$  that are around 11%–14% lower than those in birds flying alone. If a similar reduction occurs in barnacle geese flying in formation, this would equate to a potential energy saving of approximately 25%, according to calibration equation (3). There is, however, no evidence at present that the wild migrant barnacle geese actually flew in such flocks for much of their migration, or that they obtained any such aerodynamic advantage during flapping flight.

Clearly, it is necessary to conduct further wind tunnel- and field- based studies in order to clarify the detailed relationship between  $f_H/VO_2$  and investigate the differences, particularly in  $f_H$ , between wild and captive birds. Even so, both the wind tunnel and mass-loss data for barnacle geese, and the inter-species allometric relationship of  $VO_2$  for 9 different species of birds (mass-specific minimum  $VO_2 = 173$ ,  $M_b^{-0.224}$ ,  $r^2 = 0.848$ ; Bishop et al., 2002), support the conclusion that the mass-specific minimum power cost of forward flapping flight for larger species of birds appears to be remarkably low. For barnacle geese, this value lies between a minimum of 121 and a maximum of  $163 \text{ ml min}^{-1} \text{ kg}^{-1}$ .

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