Polar Biol (2000) 23: 812–816

ORIGINAL PAPER

Charles M. Drabek · Yann Tremblay

Morphological aspects of the heart of the northern rockhopper penguin (*Eudyptes chrysocome moseleyi*): possible implication in diving behavior and ecology?

Accepted: 20 May 2000

Abstract We compared the heart morphology of the small, deep-diving northern rockhopper penguin to the hearts of small, shallow-diving and large, deep-diving penguin species. The rockhopper penguin had a heart larger than expected for its body mass, and its heart weight/body weight was significantly greater than in the larger Adélie penguin. We found the rockhopper's right ventricle weight/heart weight to be significantly greater than this relationship in both the larger chinstrap and Adélie penguins. The relationship of the right to left ventricular weights in the rockhopper heart is not different to that of the large, deepest-diving emperor penguin. A larger heart in the rockhopper penguin might be related to its diving behavior and ecology if it contributes to diving efficiency during foraging by increasing lung perfusion during surface recovery. This would lead to decreased surface time.

Introduction

Although it has been three decades since Kooyman et al. (1971) reported on a pathfinding investigation of determining the behavior of freely diving penguins, it has only been in the last 10 years that biologists have used similar and even more sophisticated techniques (e.g., Kooyman and Kooyman 1995) to elucidate the diving capabilities of most of the 18 penguin species. Excellent reviews of these studies are numerous (Burger 1991; Wilson 1995; Kooyman and Ponganis 1997; Schreer and Kovacs 1997; Kooyman and Ponganis 1998). Drabek (1989) published the first suggestion that the heart morphology of penguins might play a role in their diving capabilities. He noted that the penguin heart size relative to body mass (heart ratio) was larger than expected for birds and that the right ventricle of the emperor penguin (*Aptenodytes forsteri*) was more muscular in proportion to both the left ventricle and the heart than that of the chinstrap (*Pygoscelis antarctica*) and Adélie penguins (*P. adeliae*). The long, deep diving capabilities of the emperor penguin have long been documented (Kooyman et al. 1971), and Drabek (1989) suggested the heart morphology might contribute to diving efficiency during feeding by increasing lung perfusion to decrease surface recovery times between dives. In a subsequent study, Drabek (1997) compared and contrasted the heart morphology of these deep-diving penguin species with that of the little penguin (*Eudyptula minor*). The little penguin represents the smallest of all the penguin species and is known to be a brief, shallow diver (Bethge et al. 1997). Drabek reported that the little penguin heart is not larger than expected for its body mass and that the right ventricle relative to the heart and left ventricle is significantly less muscularized than right ventricles in the larger, deeper-diving penguin species. Tremblay et al. (1997) reported the first data on maximum diving depths attained by the northern rockhopper penguin, (*Eudyptes chrysocome moseleyi*), at Amsterdam Island. They found that although it is the third smallest (to the little penguin and Galapagos penguin) (2.3 kg), it is capable of diving deeply (168 m). This is nearly the depth (175 m) attained by the Adélie penguin (Whitehead 1989), a penguin twice the body mass of the rockhopper. More recently, Cherel et al. (1999) showed that the most remarkable feature of diving behavior in northern rockhopper penguins was the high percentage of the time spent diving (69% of their time at sea), which was mainly due to a high dive frequency (44 dives per hour at sea).

The purpose of this study was to describe the heart and ventricle sizes of the northern rockhopper and to

C. M. Drabek (✉)
Biology Department, Whitman College,
Walla Walla, Washington 99362, USA
e-mail: drabek@whitman.edu

Y. Tremblay
Centre d'Etudes Biologiques de Chizé,
U.P.R. 1934 du Centre National de
la Recherche Scientifique,
79360 Villiers-en-Bois, France

make comparisons with the hearts of the smaller, shallow-diving little penguin and with the large, deep-diving Antarctic penguins.

Materials and methods

The hearts of seven male and four female adult northern rockhopper penguins (*E. chrysocome moseleyi*) from Amsterdam Island (37°50′S, 77°31′E) in the southern Indian Ocean were weighed and measured. The hearts were removed from autopsied penguins that had died from natural causes (mainly predation) near the colonies. The hearts were initially fixed in 10% formalin and stored in 30% isopropyl alcohol until measurements were taken. Since the hearts were not weighed upon removal, there was no check made of any influence of the preservatives. This was the same protocol followed by Drabek (1989, 1997). The brachiocephalic artery and pericardium were removed and excess alcohol was wicked away before the weights were recorded on an Ohaus triple-beam balance to the nearest 0.1 g. Helios needle calipers were used to measure the length of the heart from the apex to the orifice of the pulmonary valve. The circumference and width were measured at the greatest breadth of the ventricles. Measurements were made to the nearest 0.1 mm. The left ventricle weight included the interventricular septum. The differences between the means were compared using Student's *t*-test and ANOVA. The 5% level of probability was accepted as indicating statistical significance.

Results

Table 1 shows the heart measurements for the rockhopper penguin in comparison to those of the little, emperor, chinstrap, and Adélie penguins. The length/width relationship of the rockhopper's heart was significantly different from this relationship in the emperor's heart ($F_{4,57} = 5.36$, $P < 0.001$). The rockhopper's heart is proportionately wider. The heart weight relative to the body weight of the rockhopper penguin is no different from that of the chinstrap but significantly greater ($P < 0.001$) than in both the Adélie and little penguins (Fig. 1). In the rockhopper, the weight of the right ventricle relative to the weight of the left ventricle is no different from this relationship in the emperor but significantly greater ($P < 0.001$) than in the little, chinstrap, and Adélie penguins. The weight of the right ventricle relative to the heart weight in the rockhopper penguin is significantly less ($P < 0.001$) than this relationship in the emperor and significantly greater ($P < 0.001$) than in the little, chinstrap, and Adélie penguins.

Discussion

The general anatomical aspects of the cardiovascular morphology of penguins have been described in several investigations (Watson 1883; Pycraft 1907; Glenny 1944, 1947; Andrews and Andrews 1976). Drabek (1989) was the first to publish heart and ventricular weight data for any penguin species and the first to suggest that the heart morphology might influence diving capabilities. Drabek's (1997) heart study of the little penguin elucidated the differences between the heart anatomy of a shallow-diving penguin and the hearts of penguins known to be deeper divers. He felt the proportionately larger right ventricle contributes to diving efficiency by increasing lung perfusion during surface recovery.

Tremblay et al. (1997) recorded a dive depth of 168 m for the northern rockhopper and compared their data to the allometric equation ($y = 47.6 + 18.0x$) used by Wilson (1995) to relate maximum diving depth (x) to a penguin's body mass (y). The 2.66-kg rockhoppers Tremblay et al. studied would be predicted to dive to a maximum of only 95 m, and Wilson's equation indicates that only a penguin 3 times heavier (6.69 kg) would have the ability to dive to 168 m. Even by considering usual

Table 1 The heart parameter data for the rockhopper penguin are presented as means ± standard error, with ranges *in parentheses*. The little penguin data are from Drabek (1997) and the emperor, chinstrap, and Adélie data are from Drabek (1989) (*H* heart mass; *B* body weight; *L* heart length; *W* heart width; *RV* right ventricle weight; *LV* left ventricle weight)

Parameter	Little penguin ($N = 27$)	Emperor ($N = 8$)	Chinstrap ($N = 8$)	Adélie ($N = 8$)	Rockhopper ($N = 1$)
Body weight (g)	1188 ± 56 (780–1940)	–	3900 ± 160 (3200–4500)	4400 ± 170 (3700–4900)	2340 ± 156 (1400–2950)
Heart mass (g)	9.9 ± 0.4 (6.6–14.1)	174.8 ± 5.4 (154.9–198.0)	42.4 ± 1.1 (38.6–48.0)	37.5 ± 1.4 (29.0–42.6)	24.7 ± 1.19 (17.8–31.3)
Length (mm)	28.9 ± 0.5 (23.8–36.9)	84.9 ± 2.4 (74.0–91.9)	50.6 ± 1.1 (47.2–56.0)	50.7 ± 0.8 (47.8–55.7)	38.8 ± 0.8 (32.5–41.8)
Width (mm)	23.9 ± 0.4 (20.2–30.7)	64.7 ± 1.1 (61.9–71.1)	45.5 ± 0.9 (41.0–49.0)	46.2 ± 0.9 (42.5–49.8)	33.6 ± 1.11 (27.8–38.2)
Circumference (mm)	72.3 ± 1.3 (60.0–89.0)	180.3 ± 3.5 (163.0–190.0)	116.9 ± 1.8 (110.0–123.0)	115.6 ± 1.8 (107.0–120.0)	97.3 ± 1.65 (86–104)
H/B (%)	0.86 ± 0.04 (0.50–1.16)	–	1.07 ± 0.03 (0.90–1.20)	0.85 ± 0.03 (0.73–1.02)	1.07 ± 0.05 (0.86–1.37)
L/W	1.22 ± 0.02 (1.06–1.44)	1.31 ± 0.03 (1.18–1.43)	1.12 ± 0.03 (0.96–1.25)	1.10 ± 0.03 (1.00–1.24)	1.17 ± 0.04 (0.87–1.3)
RV/H (%)	6.7 ± 0.46 (2.9–12.2)	21.26 ± 1.21 (15.9–46.1)	9.3 ± 0.48 (7.7–11.8)	10.9 ± 0.93 (7.8–15.5)	15.97 ± 0.688 (12.78–19.58)
RV/LV (%)	17.9 ± 1.14 (6.1–28.1)	37.36 ± 2.41 (26.9–46.1)	15.8 ± 0.88 (12.4–19.2)	18.9 ± 2.15 (11.2–27.6)	33.52 ± 1.1 (27.58–38.54)

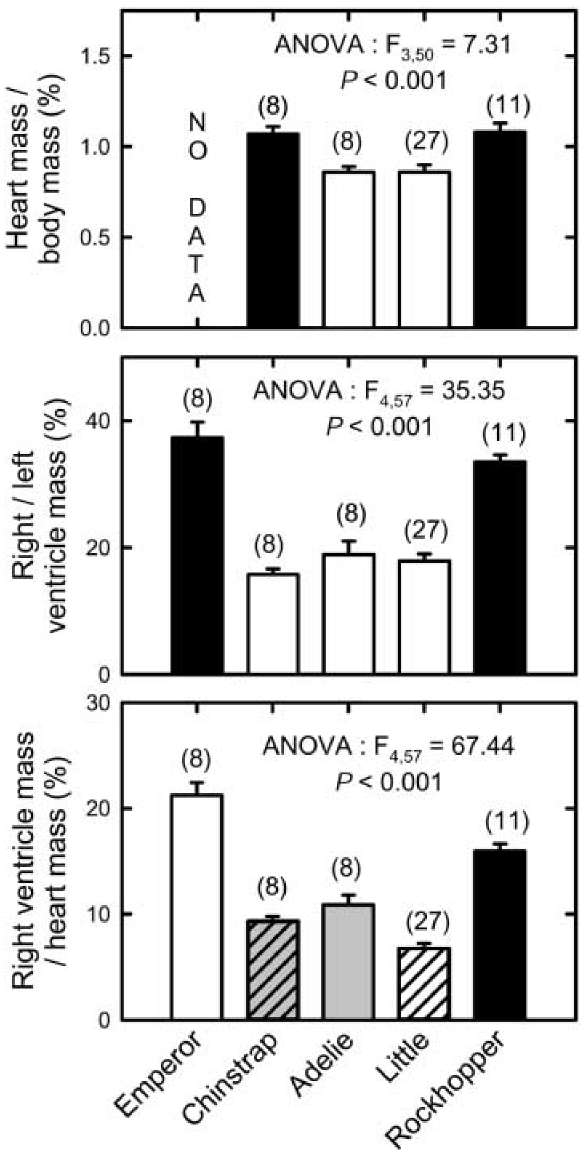

Fig. 1 Heart weight compared to body weight, and right ventricle weight compared to left ventricle weight and total heart weight in emperor, chinstrap, Adélie, little, and rockhopper penguins. Similarities in background colors or in filling patterns indicate non-significant differences, using post-hoc Tukey test. Sample sizes are given *in parentheses*

behavior instead of maximum records, the northern rockhopper penguin at Amsterdam Island spent the greater time underwater (69%) and had the higher dive frequency (44 dives per hour at sea, i.e., very short surface recovery times) among penguins (Cherel et al. 1999). These observations and our results are consistent with Drabek's (1997) assumption, and suggest that lung perfusion is particularly high in this species.

Hartman's (1955) heart weight/body weight data of 1340 hearts from 291 bird species were used by Schmidt-Nielsen (1984) to develop the following equation for expected heart size in birds: $M_{\mathrm{h}} = 0.0082\ M_{\mathrm{b}}^{0.91}$ (M_{h} and M_{b} in kilograms). Using this equation, a penguin that would be able to dive to 168 m (i.e., a 6.69-kg bird, using the allometric equation from Wilson 1995) would be predicted to have a 46.0-g heart. Our rockhopper heart specimens averaged 24.72 g in weight. We also used Schmidt-Nielsen's (1984) equation to find that the average ratio of the observed heart size to the expected heart size in our 2.3-kg rockhopper penguin is 1.43. This indicates the northern rockhopper has a larger heart than predicted for its body size. This ratio is significantly greater than is this relationship in both the 4.4-kg Adélie penguin ($t = 2.98$, $P < 0.05$) and the 1.2-kg little penguin ($t = 4.69$, $P < 0.001$), but it is not significantly different from the 1.47 ratio of the larger 3.9-kg chinstrap (Drabek 1989, 1997).

Johnston (1963) compared the heart weight/body weight of 77 species of arctic birds in Alaska and concluded that body weight was probably the most important factor influencing heart size in birds. He also noted that both his and Hartman's (1955) data suggest that birds at higher latitudes and flying birds have proportionately larger hearts. He attributed the latter to a greater energy requirement for flying than for diving. When one applies these observations to the penguins, the small northern rockhopper would be expected to have a proportionately small heart due both to its relatively small body size and to its distribution in low latitudes. Next to the little penguin and the Galapagos penguin, the rockhopper is the smallest of all penguin species. The rockhopper's distribution includes comparatively low latitudes. Williams (1995) noted its range extended north of 60°S to Amsterdam Island (37°50′S) and to Tristan da Cunha (37°S), which is the most widespread distribution in *Eudyptes* penguins. The larger emperor, chinstrap, and Adélie penguins all have distributions south of 50°S. We can expect that the heart characteristics of a rockhopper penguin provide a higher flexibility for its diving behavior. This would permit them to feed in more diverse and variable marine environments.

Table 2 shows the few penguin species for which both heart data and diving capabilities are known. Since dive depths measured by capillary tubes tend to over-estimate maximum depths in comparison to dives measured with time-depth recorders (TDRs), the observed maximum depths listed were recorded with TDRs. Bethge et al. (1997) reported that the little penguin spent 60% of its time swimming, but only 16.4% of its time was spent diving. In contrast, Cherel et al. (1999) found that the rockhopper penguin spent an estimated 80–90% underwater (diving and swimming) when at sea, 69% of which was diving to ≥3 m.

The right ventricular hypertrophy we find in the northern rockhopper penguin might be a result of an increase in the pulmonary vascular resistance. Currie (1999) reported right ventricular hypertrophy in chickens is associated with pulmonary hypertension. A larger heart may allow for a relative increase in cardiac output and gas exchange and lead to decreased time spent at the surface to refresh oxygen stores (P. Ponganis, personal communication). The relatively large heart/body mass

Table 2 The relationships between the predicted maximum depth (Wilson 1995) with the observed (TDR recordings) and the predicted heart weight (Schmidt-Nielsen 1984) with the observed heart weight of penguins

Species	Body weight (g)	Predicted max. depth (m) (Wilson 1995)	Observed max. depth (m)	Observed predicted	Mean observed heart weight (g)	Mean predicted heart weight (g) (Schmidt-Nielsen 1984)	Mean observed predicted	Reference
Little penguin	1188	68.9	27	1.00	9.9	9.6	1.03	Drabek (1997) Bethge et al. (1997)
Rockhopper	2340	89.7	109	1.22	24.7	17.77	1.39	This study Cherel et al. (1999)
Chinstrap	3900	117.8	121	1.03	42.4	28.29	1.49	Bengtson et al. (1993) Drabek (1989)
Adélie	4400	126.8	98	0.77	37.5	31.57	1.19	Drabek (1989) Chappell et al. (1993)
Emperor	25000	497.6	534	1.07	174.8	153.4	1.14	Drabek (1989) Kooyman and Davis (1987) Kooyman and Kooyman (1995)

ratio we observed for the rockhopper penguin may allow this species to more quickly refresh oxygen stores compared to other species. As a consequence, the percentage of time spent underwater should be high. Cherel et al. (1999) found that 69% (range 53–79%) of the foraging trip duration was spent diving. Since only dives ≥3 m were taken into account, this value is underestimated, and the total time underwater (diving plus swimming between 3 m depth and the surface) may attain 80–90%. In contrast, the highest recorded value for total percentage of time spent underwater comes from Bethge et al. (1997) who reported that the little penguin spent 60% of its time "active at sea" (swimming plus diving), but only 16.4% of its time was spent diving. The rockhopper penguin exhibits both the higher percentage of foraging trips underwater and the higher diving rate among penguins.

Time spent at the surface to refresh oxygen stores may be particularly reduced compared to other species. As the quantity of oxygen to restore depends on the amount of time spent in apnea, surface time needs to be compared in relation to the preceding dive duration (Kooyman and Kooyman 1995). The best index to compare the recovery time between species is the slope of the regression line of the post-dive interval (surface time) against the preceding dive duration. The steeper the slope, the more time the birds need to recover from a given time spent in apnea. Unfortunately, these data are rarely directly available in the literature. For the northern rockhopper penguin, the slope was equal to 0.12 (unpublished data, data set from Cherel et al. 1999). From the emperor penguin publication of Kooyman and Kooyman (1995), we excluded extended post-dive intervals and graphically determined a slope of about 0.28. For the seven Adélie penguins with a positive relationship between post-dive interval and diving duration, studied in Watanuki et al. (1993), the mean of the slopes was 0.32 ± 0.15. Finally, we graphically determined that the minimum slope was approximately 0.32 for the little penguin, but "most of the surface intervals were more or less equal to the preceding dive duration", i.e., the slope was more or less equal to 1.0 (Bethge et al. 1997). These scarce data tend to confirm that northern rockhopper penguins are able to recover particularly quickly from a dive compared to other species for which data are available (about 2.5 times more quickly). This characteristic of the rockhopper's diving behavior is likely to be related to the relatively large heart/body mass ratio. If that is true, we can predict that the chinstrap penguin (which has a heart/body mass ratio equivalent to that of the rockhopper penguin) is able to recover as quickly as the rockhopper. This assumption needs to be verified, since no data about surface recovery times for the chinstrap are available.

As more comparative heart data for penguins are reported, it may become more apparent if larger hearts and larger right ventricles are characteristic of those species that require less post-dive recovery time. It would be interesting to compare our northern rockhopper heart data with heart data from royal penguins. The royal penguin is nearly twice as large as the rockhopper but is not known to dive as deeply as the rockhopper. Their diving behaviors may differ since Hull's (1999) study suggests that on Macquarie Island their trophic niches do not overlap substantially.

Acknowledgements The authors thank Whitman College for its support. We are also grateful to Jean-Marc Salles for collecting samples, and to the Institut Francais Pour la Recherche et la Technologie Polaires (I.F.R.T.P.) and the Terres Australes et Antarctiques Francaises (T.A.A.F.) for logistical support. We acknowledge the constructive criticisms of the reviewers.

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