

HEART RATES AND ABDOMINAL TEMPERATURES OF FREE-RANGING SOUTH GEORGIAN SHAGS, *PHALACROCORAX GEORGIANUS*

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Summary

The South Georgian shag (*Phalacrocorax georgianus*) shows a remarkable diving ability comparable to that of penguins, yet nothing is known of the physiology of these birds. In this study, heart rates and abdominal temperatures were recorded continuously in four free-ranging South Georgian shags using an implanted data-logger. A time–depth recorder was also attached to the back of the implanted birds to record their diving behaviour.

The diving behaviour of the birds was essentially similar to that reported in other studies, with maximum dive durations for individual birds ranging between 140 and 287 s, and maximum depths between 35 and 101 m. The birds, while at the nest, had a heart rate of 104.0 ± 13.1 beats min^{-1} (mean \pm S.E.M.) and an abdominal temperature of 39.1 ± 0.2 °C. During flights of 221 ± 29 s, heart rate and abdominal temperature rose to 309.5 ± 18.0 beats min^{-1} and 40.1 ± 0.3 °C, respectively. The mean heart rate during diving, at 103.7 ± 13.7 beats min^{-1} ,

was not significantly different from the resting values, but the minimum heart rate during a dive was significantly lower at 64.8 ± 5.8 beats min^{-1} . The minimum heart rate during a dive was negatively correlated with both dive duration and dive depth. Abdominal temperature fell progressively during a diving bout, with a mean temperature at the end of a bout of 35.1 ± 1.7 °C.

The minimum heart rate during diving is at a sub-resting level, which suggests that the South Georgian shag responds to submersion with the ‘classic’ dive response of bradycardia and the associated peripheral vasoconstriction and utilisation of anaerobic metabolism. However, the reduction in abdominal temperature may reflect a reduction in the overall metabolic rate of the animal such that the bird can remain aerobic while submerged.

Key words: diving, flying, heart rate, body temperature, thermoregulation, metabolism, Phalacrocoridae, shag, *Phalacrocorax georgianus*.

Introduction

The South Georgian shag (*Phalacrocorax georgianus* Lönnerberg) is a foot-propelled pursuit diver (Ashmole, 1971) that feeds on benthic-dwelling fish. It is capable of diving to considerable depths (maximum 116 m; Croxall *et al.* 1991) and for long durations (maximum 5.2 min; Wanless *et al.* 1992), yet retains the ability to fly. The birds exhibit distinct patterns in their diving behaviour and can be categorized as being short, shallow divers (diving for ≤ 120 s and to < 20 m), long, deep divers (diving for > 120 s and to > 35 m) or mixed divers (Croxall *et al.* 1991; Wanless *et al.* 1992). These two studies have estimated that over 50% of all dives made by the South Georgian shag are for longer than their estimated aerobic dive limit (ADL; Kooyman *et al.* 1983). Thus, the inference is that the birds must obtain a proportion of their energy requirements *via* anaerobic metabolism. This would be consistent with the theory of Ydenberg and Clark (1989) that a pursuit-diving bird will resort to anaerobic metabolism to increase dive duration and hence foraging time. However, it must be remembered that

the calculations of ADL are based on a number of estimates (e.g. the diving metabolic rate) that have rarely been tested and have certainly never been tested in the South Georgian shag.

Studies investigating the effect of forced diving on the physiology of cormorants, *P. auritus*, in the laboratory (Mangalam and Jones, 1984; Jones and Larigakis, 1988) found that submergence caused a profound bradycardia. This cardiac response indicates that the cormorant undergoes extensive peripheral vasoconstriction and switches to anaerobic metabolism in the underperfused tissues (Irving, 1939). If wild birds also resort to anaerobic metabolism, as is indicated when they exceed their estimated ADL, then they too may show this cardiac response.

However, ducks rarely exhibit a bradycardia when diving voluntarily (Butler and Woakes, 1979; Furilla and Jones, 1987) and the blood supply to the active muscles is maintained at the same level as when exercising in air (Bevan and Butler, 1992b), indicating that they are metabolizing aerobically.

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Bradycardia and, presumably, its associated peripheral vasoconstriction occur in voluntarily diving ducks only in response to external factors such as access to the surface being temporarily denied (Stephenson *et al.* 1986) or when being chased.

Penguins are extremely well adapted to their aquatic existence, e.g. they have reduced pneumatization of the bones to reduce buoyancy and increased subcutaneous fat deposition for insulation. However, these adaptations also mean that they have lost their flight capabilities. The South Georgian shag, as well as having a considerable diving ability that is surpassed only by that of the larger penguin species, retains its ability to fly, which is a highly aerobic activity. This dual lifestyle is further complicated because the birds use their wing muscles for flight and their leg muscles for underwater propulsion and, therefore, both sets of muscles must be well developed. They also do not appear to possess a substantial fat layer to aid insulation (R. M. Bevan, personal observation), as in the penguins, and therefore must use other thermoregulatory mechanisms to control body temperature.

How are these birds capable of such an amazing diving ability? The purpose of the present study was to record heart rate and abdominal temperature continuously in free-ranging South Georgian shags. These measurements were then related to the behaviour of the bird in the field, with particular attention being given to the physiological responses to diving and flying.

Materials and methods

Birds and study site

The study was undertaken at the British Antarctic Survey (BAS) base on Bird Island, South Georgia (54°S, 38°W) during the 1992–1993 austral summer. Four South Georgian shags (SGS1–4) were used in the present study, two females and two males (mean mass 2.39±0.09 kg; S.E.M.) from different nests, which were brooding/rearing 1–3 chicks.

Heart rate data-loggers

Heart rates and abdominal temperatures of the free-ranging birds were determined using heart rate data-loggers (HRDL; Woakes *et al.* 1995). The HRDLs weighed 19 g or approximately 0.8% of body mass. They were programmed to record the number of heart beats in every 15 s period and to take a reading of abdominal temperature every 60 s (for bird SGS4, abdominal temperature was recorded every 30 s). Programming was achieved *via* a purpose-built interface connected to an A/D converter (PCLL-711, Advantech Co. Ltd) housed in a lap-top computer (316LT, Dell). After programming, the HRDL was encapsulated in wax and then in silicone rubber to ensure biocompatibility. The entire HRDL was sterilised in alcohol before implantation.

The birds were caught at the nest site and transported back to the operating facilities (approximately 1 km distance) where they were anaesthetised with a halothane-enriched air:O₂ mixture (induction 1–1.25%, maintenance 0.75–1.25%). The HRDL was implanted as described by Bevan *et al.* (1995a),

the time of implantation being noted for synchronisation with a time–depth recorder (see below). A long-acting antibiotic (LA Terramycin) was injected intramuscularly into the pectoralis muscle, and the bird was transported back to the colony. It took approximately 2 h to transport the birds, implant them and return them to the colony. The study site was monitored for several hours each day, and the times of arrival and departure and periods of flying of the implanted birds were recorded.

The HRDLs had been tested previously in two other species, the gentoo penguin *Pygoscelis papua* and the Antarctic fur seal *Arctocephalus gazella*. In the gentoo penguin, a heart rate radio transmitter (Woakes and Butler, 1975) was attached to the HRDL so that both devices used the same electrocardiogram (ECG) electrodes. The dual device was encapsulated in wax and silicone rubber and was implanted into the abdominal cavity (Bevan *et al.* 1995a). The bird was then occasionally walked on a treadmill over a period of several days (Bevan *et al.* 1995b). At random intervals, the ECG was recorded from the radiotransmitter for periods of at least 2 min. The HRDL transmits a click when it recognises the ECG and so the audio signal from a receiver was recorded at the same time. There was no difference between the timing of the ECG events from the two devices. A subsequent analysis showed that the HRDL accurately counted the number of heart beats in each time period. The same was also found to be true for the tests performed with the Antarctic fur seal.

Time–depth recorders

The birds were recaptured 3–4 days after the implantation procedure and a time–depth recorder (TDR; mk V, Wildlife Computers, Inc.) was attached. The interval between the implantation procedure and TDR attachment was designed to allow the birds to recover. Previous work using HRDLs has shown that 1–2 days is sufficient. The TDR weighed 50 g and had a front cross-sectional area of 5.7 cm². The mass of the TDR was, on average, 2.1% of the body mass of the birds on capture. It was attached to the feathers on the dorsal body surface between the wings and anterior to the base of the tail using quick-drying epoxy resin (RS Components). Epoxy resin was also applied to the front of the TDR to produce a more hydrodynamic profile. The TDR was programmed to sample depth every 1 s (Boyd, 1993) and to record the periods for which the device was dry. By positioning the TDR such that the conductivity switch was distal to the head, the switch was often submerged when the bird was on the water surface and was never dry for more than a few seconds (R. M. Bevan, K. R. Reid and I. L. Boyd, personal observations). It was therefore possible to determine when the birds landed on and left the water and hence to infer when they were flying or resting ashore.

Respirometry

At the end of the monitoring period (see Table 1), the birds were recaptured and transported back to the holding facilities where the oxygen consumption of three of the birds was

measured in air and when the birds were on water. Bevan *et al.* (1994, 1995b) provide full details of the respirometry equipment used. It consisted of a Perspex respirometer with a monitored flow of air passing through it. The oxygen and carbon dioxide levels in the air entering and leaving the box were monitored using a paramagnetic O₂ analyser (Servomex 570A) and an infrared CO₂ analyser (Servomex 1410), respectively. For measurements when the bird was dry, the respirometer was placed on an inactive treadmill, whereas for measurements with the bird resting on the water, the respirometer was held above a water channel and the edges of the box were submerged to maintain a seal. The effects of resting on water on the energy expenditure, heart rate and abdominal temperature could then be determined.

Finally, the data-loggers were removed using the same operating procedure as for implantation, and the data were extracted for later analysis. The birds were then taken back to the colony and released. The colony was not monitored after the study in order to reduce any further disturbance. However, previously implanted birds which had the devices removed earlier in the study were seen feeding their chicks.

Data analysis

Diving activity

A dive was deemed to occur when the depth was greater than 2 m. The parameters calculated from the depth data (see Fig. 1) were time of dive, dive duration, maximum depth, duration of the post-dive surface interval, descent rate, ascent rate, transit time (time spent descending and ascending), time spent foraging (bottom time), dive cycle duration (a dive cycle is composed of the dive plus the subsequent surface interval) and dive bout duration (see below for definition of a bout).

Descent rate, ascent rate, descent time, ascent time and

bottom time were calculated from the depth data using a modified version of the iterative regression described by Yeager and Ultsch (1989) and Nickerson *et al.* (1989). Their technique applies a two-segment analysis to a data set and thus calculates two ‘best-fit’ regressions and the point where the two lines intersect. In applying the technique to the diving data, each dive was split into two parts. For the first half of a dive, the slopes of the two regression lines calculated from the data correspond to the rate of descent (line *dr*, Fig. 1) and to the rate of change of depth while at the bottom (line *br1*, Fig. 1). As the abscissa is time, the point of intersection is equivalent to the time that the descent phase (*dt*) finishes and foraging time begins. For the second half of the dive, the slopes of the regression lines correspond to the rate of change of depth while at the bottom (line *br2*, Fig. 1) and the rate of ascent (line *ar*, Fig. 1). The point of intersection is the time at which foraging ends and ascent (*at*) begins. The time spent in the foraging area (bottom time) is the difference between the time at which the bird finished its descent and that at which it started to ascend (*bt*). The minimum duration of a dive for this analysis to be carried out was 13 s, because this was the time required to fulfil the requirements for the sample size of each regression.

The diving behaviour of the birds was split into discrete bouts. To determine the bout-ending criterion (BEC) of each individual, a log-survivor curve of the surface interval data was plotted (Gentry and Kooyma, 1986). The BECs for birds 1, 2 and 3 were surface intervals >255 s, >358 s and >322 s, respectively. Bird 4 showed two clear inflections in the log-survivor curve at 122 s and 856 s. Visual inspection of the data suggested that these BECs were correct (see Croxall *et al.* 1991) and that the larger BEC of bird 4 occurred when dives were for longer durations (>180 s).

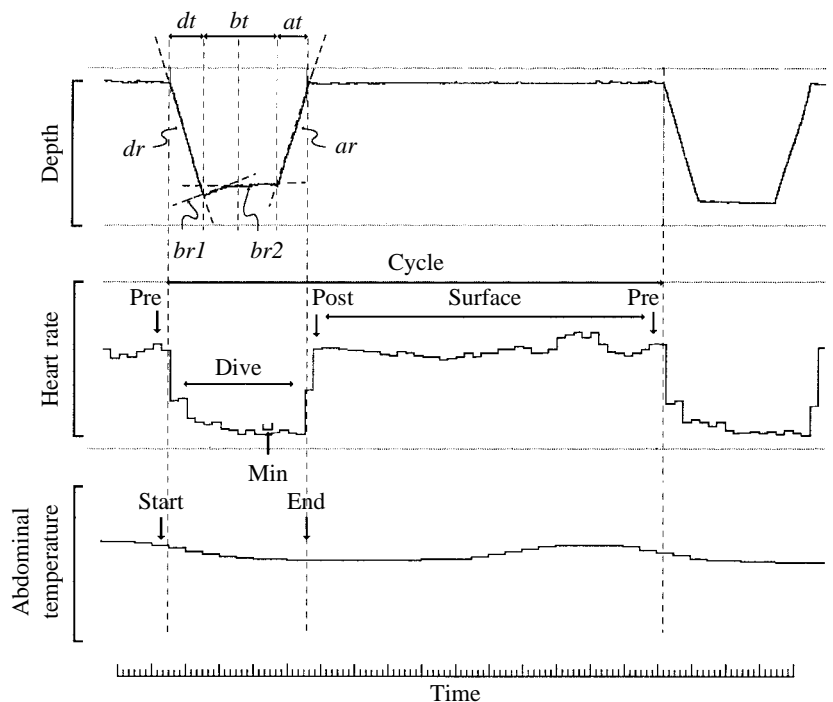


Fig. 1. Diagram explaining how the diving depth, heart rate and abdominal temperature data were analysed for each diving cycle. Depth: *dt*, descent phase; *bt*, bottom/foraging time; *at*, ascent phase; *dr*, slope of regression line, equivalent to rate of descent; *br1* and *br2*, slopes of regression lines, equivalent to rates of depth change at the bottom; *ar*, slope of regression line, equivalent to rate of ascent. Heart rate: Pre, pre-dive heart rate; Dive, mean heart rate during submersion; Post, post-dive heart rate; Surface, mean heart rate while at the surface between dives; Min, minimum heart rate during a dive. Abdominal temperature: Start, temperature at the start of a dive; End, temperature at the end of a dive. The time axis is in minutes. For further details see text.

Heart rate

A number of different heart rate parameters were calculated using the depth data as a guide (see Fig. 1). These were pre-dive heart rate, mean heart rate during diving, post-dive heart rate, mean heart rate while at the surface between dives, minimum heart rate during a dive, heart rate over each dive cycle and mean heart rate over each dive bout. As the sampling rates of the HRDL and TDR were different, it was not possible to synchronise the two data sets exactly. In addition, the HRDL stored the number of beats over 15 s periods. Therefore, the first heart rate measurement taken after the start of the dive (Fig. 1) may include a proportion of the heart beats which occurred during the pre-dive period and a proportion that occurred during the dive. Likewise, the heart rate measurement taken at the end of the dive may include a proportion of heart beats which occurred during the dive and a proportion occurring during the surface interval. To circumvent this problem, heart rates were analysed during diving only if the dive duration was greater than 59 s. The first heart rate measurement during diving to be analysed was the first taken when a full 15 s (the sampling frequency of the HRDL) of heart rate counting during a dive had elapsed. Similarly, the last analysed heart rate of a dive was taken before surfacing. Consequently, if a dive lasted 60 s and started 5 s into the HRDL sampling regime, three heart rate measurements were used: the first covering the period 10–24 s, the second covering the period 25–39 s and the final measurement covering the period 40–54 s. The mean of these gives the mean heart rate during the dive. A similar analysis was also applied to the surface intervals (Fig. 1). Through this mode of analysis, it was hoped to eliminate the effects of surfacing and diving when substantial changes in heart rate may occur (Butler and Woakes, 1979).

The temporal changes in heart rate with dive duration were analysed without the above restrictions. The heart rate value that occurred when diving started was used as time 0; thereafter, the heart rate values were plotted with respect to this timing.

Table 1. Summary of basic information on the South Georgian shags *Phalacrocorax georgianus* studied

Bird	Sex	Chicks ^a	Date ^b		Duration ^c (h)	Mass ^d (kg)	
			Implanted	Removed		Start	End
SGS1	F	3	17/1/93	22/1/93	124.2	2.22	2.01
SGS2	M	1	18/1/93	24/1/93	146.1	2.58	2.76
SGS3	F	1	23/1/93	29/1/93	134.4	2.26	2.26
SGS4	M	2	26/1/93	1/2/93	149.6	2.50	2.58
Mean					138.6	2.39	2.40
S.E.M.					5.8	0.09	0.17

^aNumber of chicks in nest.

^bDates when logger was implanted and removed.

^cDuration of monitoring period.

^dMass of bird on first capture and at the end of the monitoring period.

The minimum heart rate during a dive was the lowest value recorded during each submergence. The mean heart rate over the dive cycle was calculated from the first analysed diving heart rate up to, but excluding, the first heart rate measurement of the next dive (dive cycle heart rate was only calculated if the dive occurred within a diving bout). Pre- and post-dive heart rates were those measured during the 15 s sampling periods immediately prior to and immediately after a dive.

Abdominal temperature

The HRDL was temperature-calibrated after removal from the bird by immersing it in a water bath. The water temperature was varied between 18 °C and 42 °C and measured with a precision thermometer (± 0.02 °C). After calibration, the HRDL was plunged into cold water (15.0 ± 0.5 °C) to determine the response time. The mean time for a 90% response was 225 ± 15 s ($N=4$). However, since the HRDLs responded to any temperature change within 60 s, the temperature data were adjusted to take this time lag into account.

Statistics

Statistical testing was performed using the SYSTAT (Systat Inc.) software. Mean values are given \pm S.E.M. The 95% level was taken as statistically significant. Regression analysis was performed using a least-squares regression (Zar, 1984). Differences between two means were tested with a paired *t*-test (Zar, 1984). Differences between more than two means were tested by analysis of variance (ANOVA). If a significant difference was found to exist between more than two means, *post-hoc* tests were performed to determine where these occurred (Zar, 1984).

Results

Study birds

The mean duration of heart rate monitoring of the four birds was 138.6 ± 5.8 h (Table 1), while the mean duration of depth monitoring was 39.2 ± 8.33 h. All but one of the birds used in the present study gained or maintained body mass during this period (Table 1). There was no apparent difference in the behaviour of the experimental birds from the rest of the population, and foraging behaviour was very similar to that of unencumbered birds (Wanless *et al.* 1992). Fig. 2 shows representative traces obtained from the HRDL and TDR from two different birds.

Diving behaviour

Table 2 summarizes the diving data analysis. In total, 900 dives deeper than 3 m were recorded. SGS4 was the only bird of the present group to engage in deep (>60 m) or long (>180 s) diving activity (Croxall *et al.* 1991; Wanless *et al.* 1992). The dives from this bird were therefore also split into short (<180 s) and long (>180 s) dives for further analysis. The maximum depth attained by the individual birds ranged from 35 to 101 m. The depths and durations of dives made by individual birds were not normally distributed but were negatively skewed. The

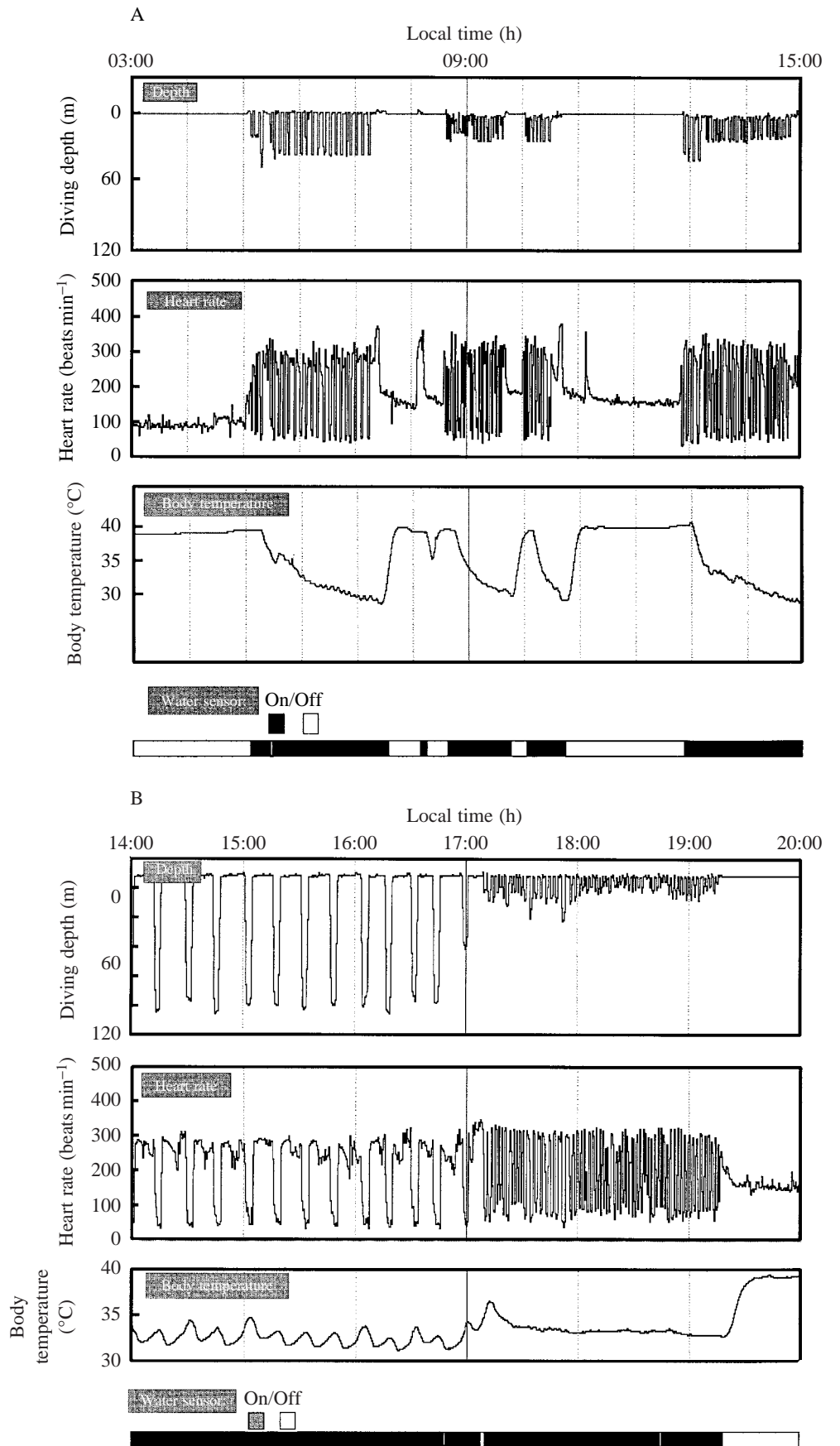


Fig. 2. Traces of diving depth (top trace), heart rate (second trace), abdominal temperature (third trace) and time spent on the water (bottom trace labelled water sensor) of (A) a female South Georgian shag (SGS1) over a 12 h period and (B) a male South Georgian shag (SGS4) while deep and shallow diving over a 6 h period.

Table 2. Summary of diving behaviour of four South Georgian shags *Phalacrocorax georgianus*

Bird	Sex	N	Depth (m)		Dive duration (s)		Median surface duration (s)	Mean descent rate (m s ⁻¹)	Mean ascent rate (m s ⁻¹)	Mean bottom ^a time		Mean transit ^a time	
			Max.	Med.	Max.	Med.				(s)	(%)	(s)	(%)
SGS1	F	65	35	28	140	115	148	1.37	1.67	82.3	73.8	28.9	26.2
SGS2	M	135	53	33	176	119	160	1.61	1.74	92.8	73.3	32.4	27.1
SGS3	F	497	41	14	156	50	43	1.36	1.63	68.7	72.0	19.5	28.0
SGS4	M	203	101	12	287	54	50	1.11	1.18	56.0	66.2	35.6	33.8
<180 s ^b		172	39	10	128	48	46	0.98	1.11	41.4	69.8	16.4	30.2
>180 s		31	101	95	287	244	667	1.51	1.35	121.2	49.9	121.3	50.1
Mean ^c			58	21.8	190	85	100	1.36	1.56	73.0	71.3	29.1	28.8
S.E.M.			15	5.2	33	19	31	0.10	0.13	9.6	1.7	3.5	1.7

^aBottom time and transit time are expressed both in seconds and as a percentage of dive duration.

^bDives of SGS4 were split into long (>180 s) and short (<180 s) dives.

^cThe mean and standard error were calculated from the mean for each individual bird.

Ascent rate, descent rate, bottom time and transit time were calculated only if a dive exceeded 13 s.

mean median depth was 22±5 m and the mean median dive duration was 85±19 s (range 50–119 s). For SGS4, the median dive duration for dives lasting more than 180 s was 244 s.

Diving activity only occurred between 04:27 h and 20:11 h local time, i.e. during the hours of daylight and, although it could be split into bouts (see Table 3), these bouts were not confined to specific times of the day. There was no correlation between dive depth or duration and time of day.

Each bird showed a highly significant positive correlation between dive duration and maximum depth ($P<0.001$, mean $r=0.98±0.01$), but, although dive duration was significantly related to the duration of post-dive intervals shorter than 900 s ($P<0.001$), there was a much weaker correlation ($r=0.61±0.11$). There was also a significant, positive correlation between the time spent at the bottom and dive duration ($P<0.001$, $r=0.97±0.02$). When the time spent at the bottom was expressed as a percentage of dive duration, this relationship weakened considerably ($r=0.55±0.06$) (Fig. 3). In fact, for SGS4, the percentage of the dive spent at the bottom was negatively correlated with dive duration. This was due to a reduction in the proportion of time spent at the bottom in dives lasting more than 180 s (50%) compared with dives

lasting less than 180 s (70%) (Table 2; Fig. 3). Consequently, the proportion of time spent in transit to the feeding area must be increased in dives of over 180 s.

The duration of dive bouts varied between birds (range 43.2–101.6 min, mean 68.3±12.6 min), as did the number of dives per bout (range 10.7–34.6, mean 21.2±5.3) (Table 3). The number of dive bouts per day varied between three and six, with a mean of 4.6±0.3.

Heart rate

General

A total of 133,023 measurements of heart rate were obtained from the four birds over a mean recording period of 138.6±5.8 h. For three of the four birds, heart rate was bimodally distributed, but for one (SGS2) there was a trimodal distribution (Fig. 4). The lower peak frequencies occurred at 93±5 beats min⁻¹ and the upper peak at 307±10 beats min⁻¹. The middle peak of SGS2 occurred between 152 and 159 beats min⁻¹. The mean maximum recorded heart rate was 511±48 beats min⁻¹. However, 99% of the heart rates recorded were less than 360±19 beats min⁻¹. There was a daily pattern to heart rate, common to all birds,

Table 3. Dive bout analysis of four free-ranging South Georgian shags *Phalacrocorax georgianus*

Bird	N	Duration (min)	BEC (s)	Dives per bout ⁻¹	T _b (°C)			f _H (beats min ⁻¹)
					Start	End	Δ	
SGS1	6	43.23	255	10.7	41.3	38.9	-2.4	216.2
SGS2	8	72.95	358	14.9	40.0	36.1	-3.9	244.6
SGS3	16	55.56	322	34.6	39.9	30.5	-9.4	207.3
SGS4	8	101.56	122, 856	24.9	38.7	35.0	-3.7	201.2
Mean	9.5	68.33	264 ^a	21.2	40.0	35.1	-4.9	217.3
S.E.M.	2.2	12.64	52	5.3	0.5	1.7	1.6	9.6

Duration, duration of diving bout; BEC, bout-ending criterion for post-dive interval; T_b, abdominal temperatures at the start and end of a dive bout; f_H, mean heart rate over the entire bout; Δ, difference between resting and diving abdominal temperatures.

^aExcludes data from dive bouts containing long dives from SGS4.

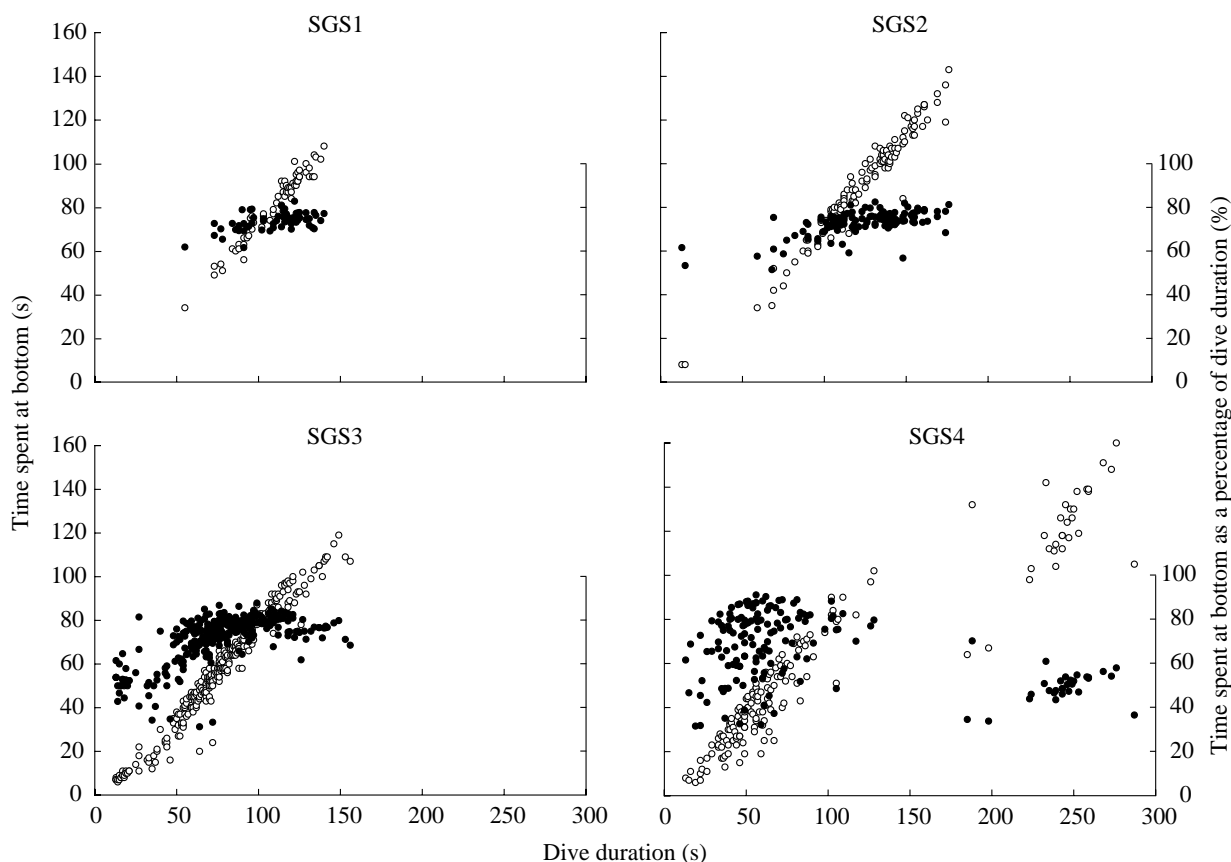


Fig. 3. Time spent at the bottom (○) and time spent at the bottom as a percentage of dive duration (●) as a function of dive duration (s) for four South Georgian shags.

Table 4. Heart rates during resting and diving of four free-ranging South Georgian shags *Phalacrocorax georgianus*

Bird	Resting	Pre	Dive	Post	Surface	Cycle	Min	t_d	N
SGS1	84.6	315.0	90.8	321.8	294.8	216.8	65.3	123	65
SGS2	142.8	292.9	143.0	314.7	283.1	238.2	81.0	118	112
SGS3	94.1	272.7	99.9	308.1	251.1	195.0	56.0	87	188
SGS4	94.6	293.1	80.9	281.4	270.8	203.1	56.8	160	77
<180 s ^a	–	299.1	81.0	293.5	273.7	192.3	64.6	88	45
>180 s	–	283.9	77.0	259.9	277.3	222.0	43.1	260	32
Mean	104.0	293.4	103.7	306.5	274.9	213.3	64.8	122	
S.E.M.	13.1	8.6	13.7	8.8	9.3	9.4	5.8	15	

Resting, mean heart rate (in beats min^{-1}) recorded during the hours of darkness.

Pre, heart rate prior to submergence; Dive, mean heart rate during submergence; Post, heart rate on surfacing; Surface, mean heart rate during surface interval; Cycle, mean heart rate over the entire dive cycle (dive + post-dive surface interval); Min, mean minimum heart rate during diving; t_d , mean dive duration (s); N , number of dives recorded.

^aDives of SGS4 were split into long (>180 s) and short (<180 s) dives.

The means and standard errors were calculated from the mean of each individual bird.

with high values occurring during the hours of daylight and low values during the night (Fig. 5). Resting heart rates were obtained when the birds were at the nest and during the hours of darkness and ranged between 85 beats min^{-1} and 143 beats min^{-1} for individual birds, with a mean of 104.0 ± 13.1 beats min^{-1} (Table 4).

Diving

The high heart rates which occurred during the day coincided with the diving activity (Fig. 5). For most birds, this was shown by an increase in heart rate between 04:00 h and 05:00 h local time. SGS4 did not dive until after 09:00 h local time, but again this was reflected by an concomitant elevation

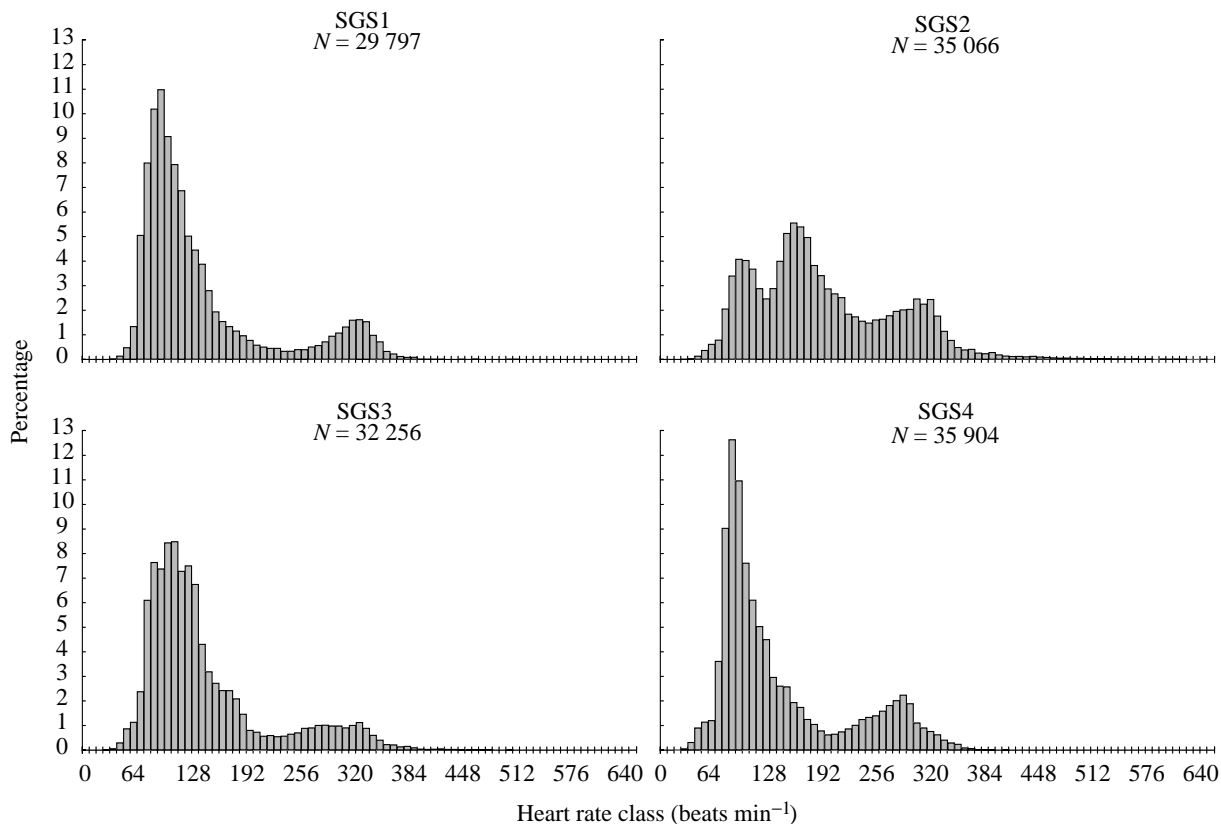


Fig. 4. Frequency distributions of heart rate (beats min^{-1}) for four South Georgian shags. Each heart rate class is expressed as a percentage of the total number of heart rate measurements from that bird (N).

in heart rate (Fig. 5). Pre- and post-dive heart rates did not differ significantly (Fisher LSD test, $P=0.370$). The pre-dive heart rate was also not significantly different from the mean heart rate measured during the surface interval ($P=0.212$), whereas the post-dive heart rate was found to be significantly higher ($P=0.039$; Table 4). The minimum heart rate recorded during a dive (64.8 ± 5.8 beats min^{-1}) was significantly lower than both the mean heart rate measured during the whole period of submersion ($P=0.013$) and the mean resting heart rate ($P=0.012$). There was no significant difference between mean heart rate during diving and that at rest ($P=0.979$).

There was only a very weak (not significant) correlation between the pre- ($r=0.06$, $P=0.266$) and post-dive ($r=-0.02$, $P=0.336$) heart rates and the depth of the succeeding or preceding dive. This was also true when the two variables were correlated with dive duration ($r=0.10$, $P=0.358$ and $r=-0.02$, $P=0.456$). The minimum heart rate recorded during diving was, however, significantly negatively correlated with both dive depth ($r=-0.53$, $P<0.001$) and dive duration ($r=0.57$, $P<0.001$, Fig. 6). The mean heart rates recorded during a dive also fell as the dive progressed (Fig. 7). In all birds, the mean heart rate at, or near, the end of the dive was below the resting level for that bird.

Flight

Periods of flights of varying durations were recorded for all

of the birds. Most flights were short and consisted only of leaving the colony and landing on the sea a few hundred metres away, or flying from the sea to a rocky outcrop. The duration of these flights was usually less than 30 s. For heart rate analysis, only flights longer than 120 s were used. These flights took place when the birds foraged at a greater distance from the colony. The absolute duration of these flights could not be ascertained as the birds flew out of sight of the observer, but the mean duration for which it was possible to follow the birds was 221 ± 29 s. Mean heart rate over this period was 309.5 ± 18.0 beats min^{-1} , which was 3.05 times the resting level (Table 5).

Abdominal temperature

Resting abdominal temperature of the South Georgian shag, measured when the birds were in the colony overnight, was 39.1 ± 0.2 °C (Table 5). It was significantly higher (paired t -test, $t=-5.222$, $P=0.014$) after flying for more than 120 s, when it had risen to 40.1 ± 0.3 °C. At the start of a diving bout, abdominal temperature was again marginally above the resting level at 40.0 ± 0.5 °C (Table 3), but this was not a significant increase. Abdominal temperature fell exponentially during a diving bout (Fig. 8) and by the end of a bout had fallen by, on average, 4.9 ± 1.6 °C (range -2.4 to -9.4 °C) (Table 3). The mean minimum abdominal temperature was 31.6 ± 2.1 °C. There was a significant

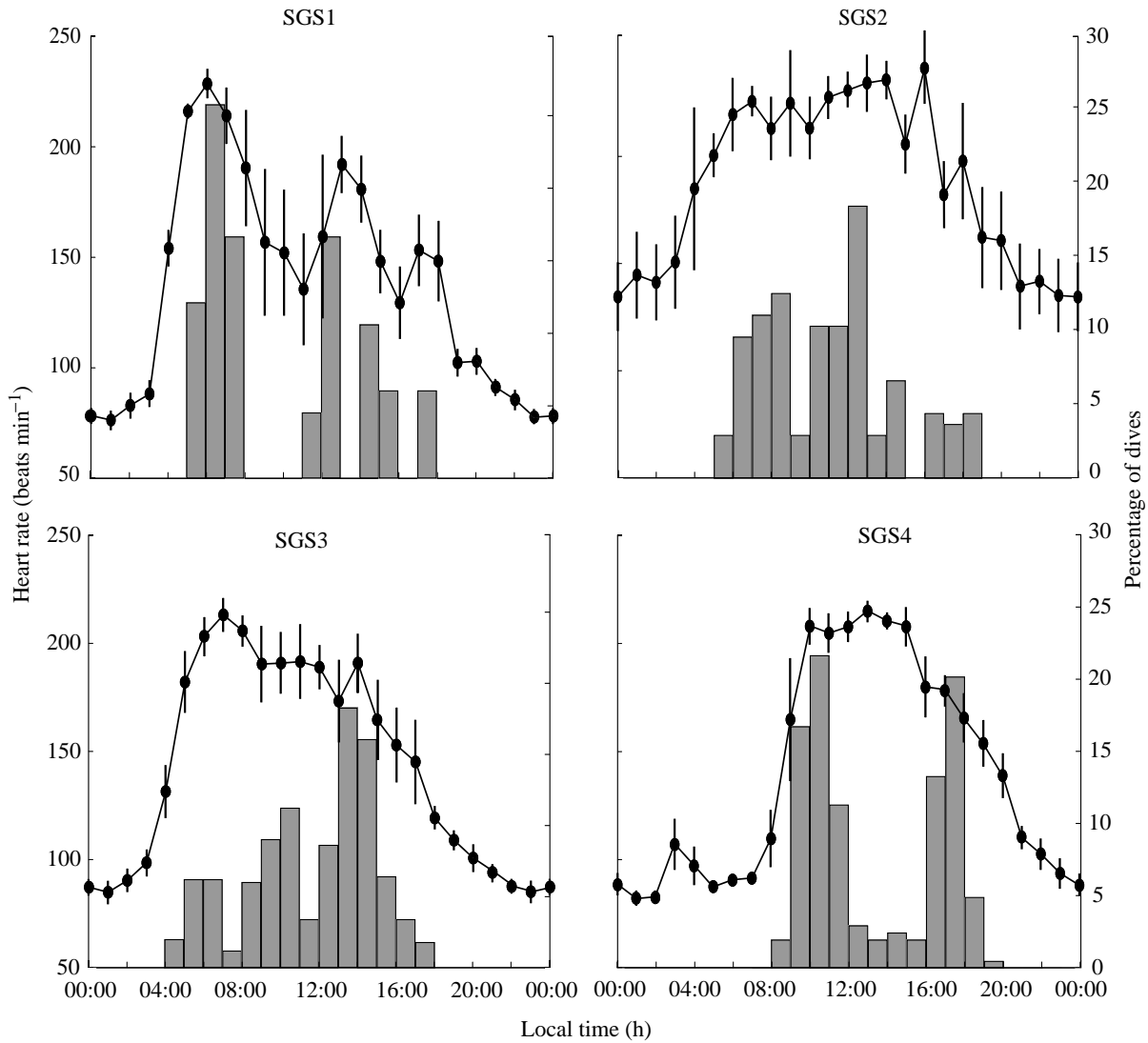


Fig. 5. Daily pattern of heart rate (beats min⁻¹) of four South Georgian shags. Each point is the grand mean calculated from the mean for each hour of monitoring from that bird. The vertical bars represents the standard error of the means. Each column represents the number of dives that occurred over that time period as a percentage of the total number of dives performed by the bird.

Table 5. Heart rates and abdominal temperatures during flight of free-ranging South Georgian shags *Phalacrocorax georgianus*

Bird	Mean duration of flight (s) ^a	N	Heart rate			Temperature		
			Resting ^b (beats min ⁻¹)	Flying (beats min ⁻¹)	Flying/resting ratio	Resting ^b (°C)	Flying (°C)	Δ
SGS1	170.0	3	84.6	267.1	3.2	39.6	40.9	1.3
SGS2	216.4	11	142.8	350.5	2.5	38.8	40.1	1.3
SGS3	195.0	10	94.1	324.2	3.4	39.0	39.5	0.5
SGS4	303.8	7	94.6	296.3	3.1	39.1	40.0	0.9
Mean	221.3	7.75	104.0	309.5	3.0	39.1	40.1	1.0
S.E.M.	29.1	1.8	13.1	18.0	0.2	0.2	0.3	0.2

^aIn visual contact with the observer.

^bResting measurements were recorded from birds during the hours of darkness.

N, number of flights recorded from that bird; Δ, difference between resting and flying abdominal temperatures.

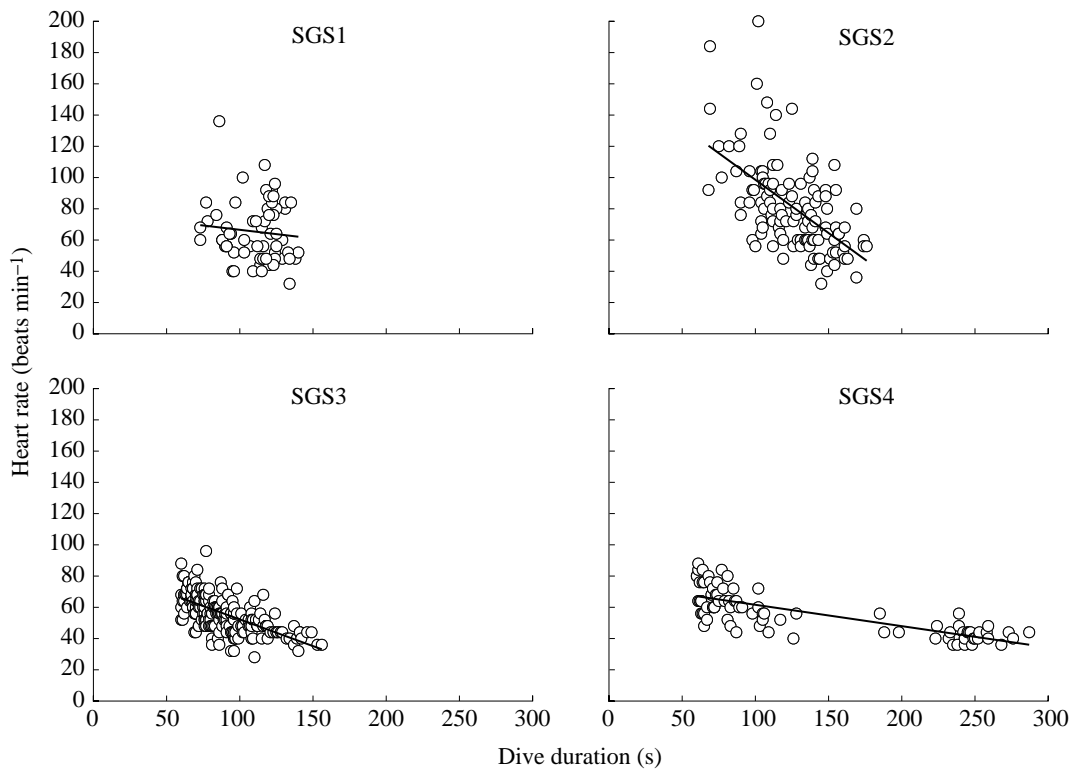


Fig. 6. Minimum heart rates (in beats min^{-1}) recorded from each dive longer than 60 s in duration as a function of dive duration (s) in four South Georgian shags. Note that, due to the way that heart rate is sampled, the minimum heart rate on a beat-by-beat basis is likely to be lower for each dive (see text for further details).

difference between the body temperature at rest, during flight and at the start and end of a diving bout (ANOVA, $P=0.008$). The temperature at the end of a diving bout ($35.1 \pm 1.7^\circ\text{C}$) was significantly lower than that at rest and that at the start of a diving bout (Tukey LSD, $P=0.044$ and $P=0.014$, respectively).

Table 6. Rate of oxygen consumption, rate of carbon dioxide production, respiratory exchange ratio, heart rate and abdominal temperature measured from three South Georgian shags when resting in air or on water

	Air	Water	Water/air ratio
\dot{V}_{O_2} ($\text{ml min}^{-1} \text{kg}^{-1}$)	17.33 ± 0.54	27.32 ± 0.51	1.58
\dot{V}_{CO_2} ($\text{ml min}^{-1} \text{kg}^{-1}$)	15.53 ± 0.85	19.30 ± 1.29	1.24
RE	0.90 ± 0.03	0.71 ± 0.06	0.78
f_{H} (beats min^{-1})	162 ± 27	238 ± 17	1.47
T_{b} ($^\circ\text{C}$)	41.7 ± 0.5	41.2 ± 0.4	0.99
T_{a} ($^\circ\text{C}$)	8.4 ± 0.7	7.2 ± 0.3	0.86
T_{w} ($^\circ\text{C}$)	—	6.9 ± 0.4	—

Air, values measured when the bird was in a dry respirometer; Water, values measured when the bird was on water.

\dot{V}_{O_2} , rate of oxygen consumption; \dot{V}_{CO_2} , rate of carbon dioxide production; RE, respiratory exchange ratio; f_{H} , heart rate; T_{b} , abdominal temperature; T_{a} , ambient temperature; T_{w} , water temperature.

Values are means \pm s.e.m., $N=3$.

Respirometry

The rate of oxygen consumption (\dot{V}_{O_2}) of three South Georgian shags in air was $17.33 \pm 0.54 \text{ ml min}^{-1} \text{kg}^{-1}$, rising by 58% when the birds were placed on water at 6.9°C (Table 6). This was similar to the percentage increase in heart rate, which rose from 162 ± 27 beats min^{-1} in air to 238 ± 17 beats min^{-1} when the birds were placed on the water, an increase of 47%. There was no change in body temperature as a result of being placed on the water. Both the heart rate and body temperature of the birds in air were elevated above the resting level of the birds when free-ranging in their natural environment (Tables 5, 6).

Discussion

The physiological measurements presented in this paper are some of the first to be recorded from a free-ranging bird that uses foot propulsion to dive. However, even though South Georgian shags use their feet to propel themselves through the water, they exhibit a diving ability that is comparable to that of the penguins (Croxall *et al.* 1991).

Diving behaviour

In general, the diving behaviour of the birds in the present study agrees with that reported by Croxall *et al.* (1991) and Wanless *et al.* (1992). The diving behaviour of three individuals (SGS1–3) classifies them as shallow or intermediate divers. None of these three birds showed the remarkable diving

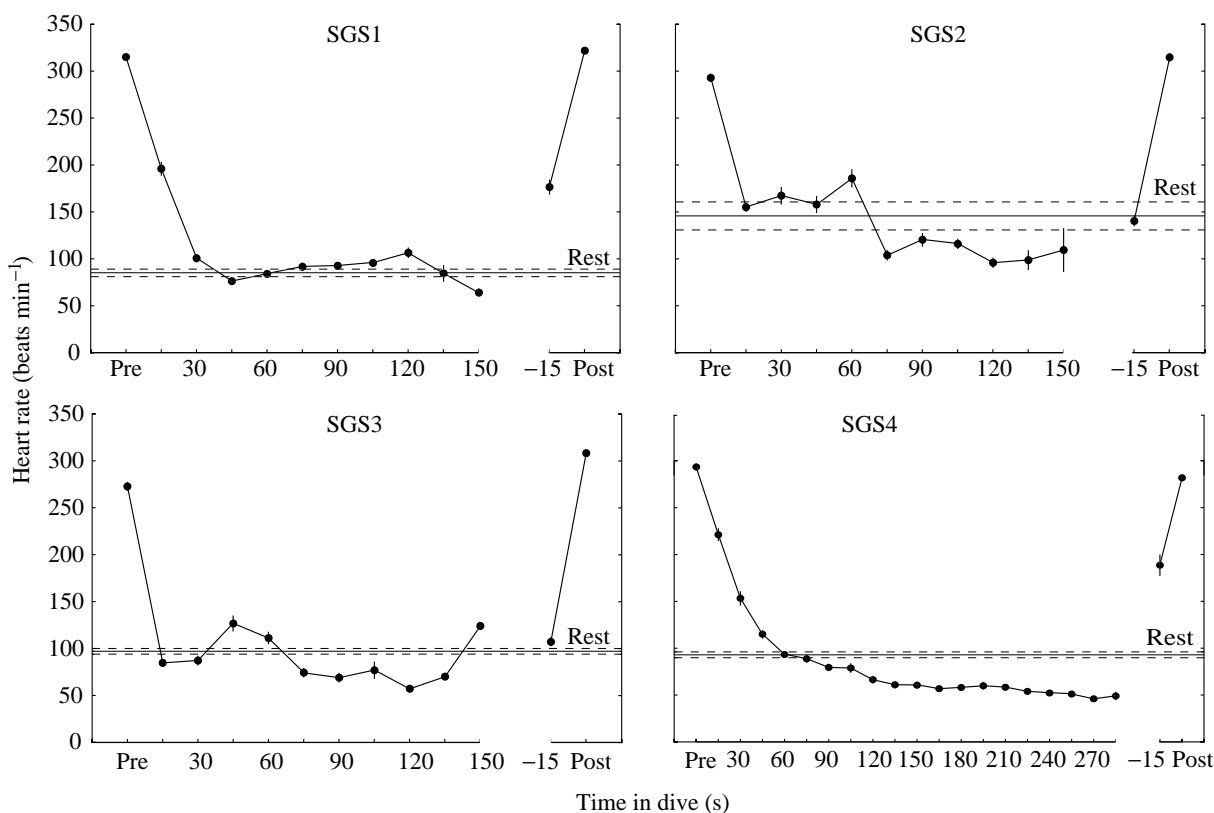


Fig. 7. Pattern of change in heart rate of four South Georgian shags during a dive. Pre is the heart rate immediately prior to submersion (see Fig. 1). All values are calculated relative to this value except for -15 s and Post values, which are the values taken 15 s before surfacing and the first measurement when the bird surfaced, respectively. Each point is the mean measured at the indicated time taken from all dives longer than 60 s for that bird. The vertical bars represent the standard error of the mean. The horizontal lines are the mean (solid line) and the standard error (dashed line) of resting values of heart rate for that individual.

performance shown by SGS4 or reported previously (Croxall *et al.* 1991; Wanless *et al.* 1992). SGS4 performed one bout consisting of 31 dives that were all deeper than 90 m and longer than 240 s. There were no other indications that this bird was remarkable in any way, and it is possible that long deep dives would have been recorded from the other birds had they been monitored for longer. In the future, it would be interesting to investigate whether the different diving behaviours described by Wanless *et al.* (1992) are confined to individuals, or whether each bird exploits all available strategies depending on the situation in which it finds itself.

The mean descent and ascent rates of all the birds (Table 2) were of a similar magnitude to those found by Croxall *et al.* (1991) but faster than those reported by Wilson and Wilson (1988). They also covered a much smaller range and they certainly did not reach the highest values of 5.0 m s^{-1} found by Croxall *et al.* (1991) or the 4.0 m s^{-1} estimated by Wilson and Wilson (1988). In the present study, a sampling rate of 1 s was chosen for the depth measurements, which provides a much more precise analysis than from sampling every 15 s (Boyd, 1993). It is likely, given the very constant rates of descent and ascent recorded in the present study, that the high rates found by others are incorrect. Indeed, these high rates represent values of approximately 10 body lengths s^{-1} , comparable with

the sustained speed attainable by salmonid fish. Interestingly, when comparing the long and short dives of SGS4, both the ascent and descent rates were higher for the long dives than for the short ones. This contrasts with the theory of Thompson *et al.* (1993) who predicted that, in seals at least, swim speed should decrease as depth of dive increases.

The mean transit times reported here are comparable with those of birds classified as intermediate divers (Croxall *et al.* 1991). However, the time spent at the bottom, equivalent to the foraging time, is more similar to the bottom time reported for the deep dives in the birds studied by Croxall *et al.* (1991). Wilson and Wilson (1988) reported a significant relationship between estimated bottom time and dive depth in two species of cormorant. This was also found in the present study, although not by Croxall *et al.* (1991). In the present study, both travel time and time spent at the bottom increased with dive duration (see Fig. 3), while the percentage of the dive time spent at the bottom increased at a much lower rate. For SGS4, the relationship was actually reversed, with the proportion of the dive spent at the bottom decreasing for longer dives. This is in agreement with the model proposed by Houston and Carbonne (1992) which predicts that the time spent in the foraging area should first increase and then decrease as travel time increases.

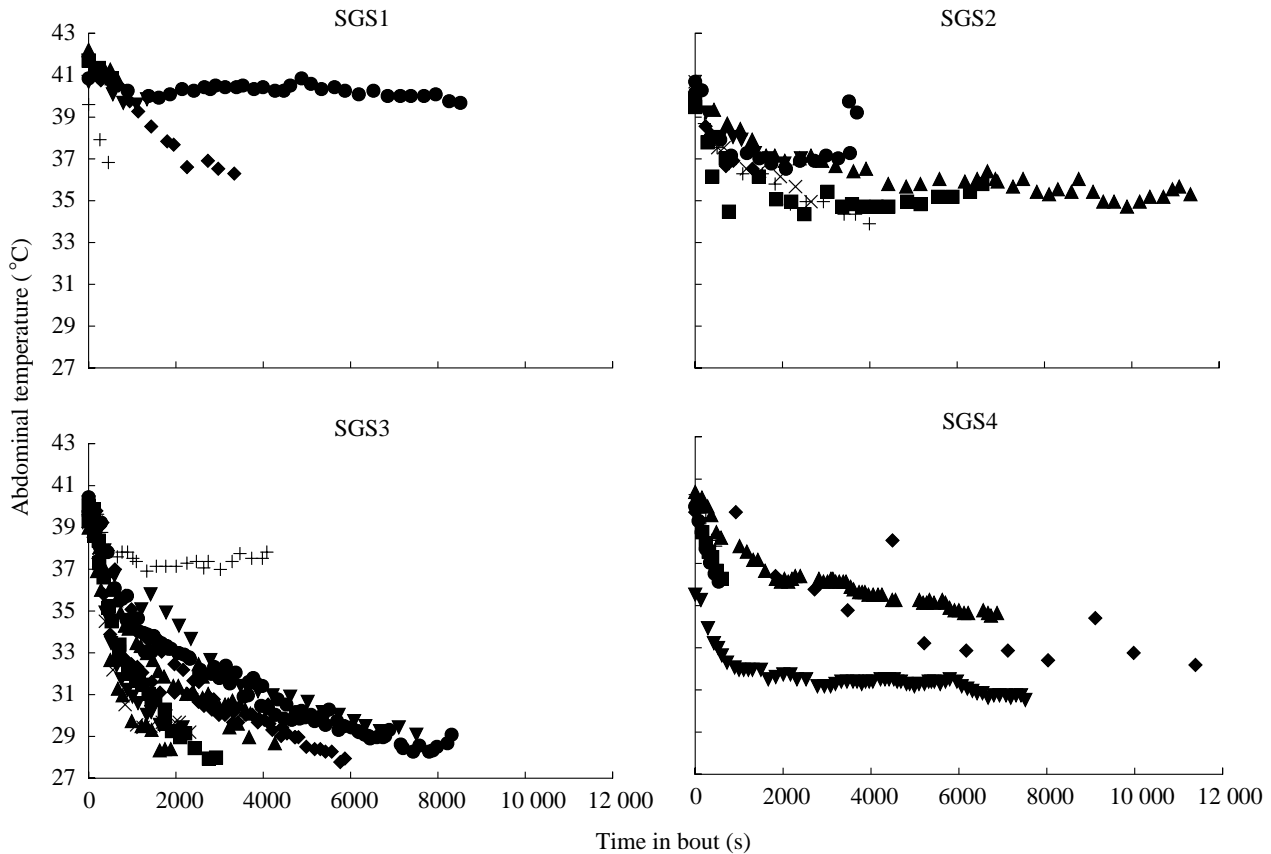


Fig. 8. Abdominal temperature ($^{\circ}\text{C}$) at the end of a dive expressed as a function of the time of the measurement within a bout of diving for four South Georgian shags. An exponential decay best describes the reduction in temperature with time. The different symbols represent different dive bouts. For SGS4, not all dives are represented in order to retain the same scale for a comparison between birds.

Heart rate

There was a distinct modality to the heart rate frequency distributions. For SGS2, there were three distinct peaks, whereas the others showed only two peaks (Fig. 4). The heart rates of the birds during diving were distinctly bimodal (see Fig. 2), a feature that is commonly seen in birds diving voluntarily in the laboratory environment (e.g. Butler and Woakes, 1979; Furilla and Jones, 1987; Stephenson *et al.* 1992) and in free-ranging gentoo penguins (R. M. Bevan, P. J. Butler, A. J. Woakes and J. P. Croxall, unpublished data). The lower peak in the heart rate frequency distributions contains both diving and resting heart rates. The middle peak shown by SGS2 was due to this bird having a very high mean resting heart rate. There are few other data with which to compare our results. Although Kooyman *et al.* (1992) recorded heart rate in unrestrained emperor penguins, *Aptenodytes forsteri*, their birds were constrained to dive from a hole cut in the ice and to which they had to return. The recording devices used could only measure heart rates up to $120 \text{ beats min}^{-1}$, which these birds have been shown to exceed (Kooyman *et al.* 1992; Kooyman and Pongannis, 1994). Other studies measuring heart rate in free-ranging diving birds and mammals have shown a similar bimodal pattern to that reported here (Fedak *et al.* 1986; Thomson and

Fedak 1993; R. M. Bevan, P. J. Butler, A. J. Woakes and J. P. Croxall, unpublished data).

The pre- and post-dive heart rates were measured immediately before and after a dive took place. However, because of the different sampling rates of the depth and heart rate data-loggers, it is likely that these partly included diving heart rates. The pre- and post-dive heart rates presented here are therefore probably lower than if they had been measured on a beat-to-beat basis (see Butler and Woakes, 1979; Furilla and Jones, 1987).

Tufted ducks, *Aythya fuligula*, in the laboratory environment show a pre-dive tachycardia. Upon submersion, heart rate initially decreases to sub-resting levels but during the remainder of the dive rises above the resting level. This is also true of cardiac output, blood flow to the exercising muscles and metabolic rate (Woakes and Butler, 1983; Bevan and Butler, 1992b). Only when the birds extend their dive duration towards their calculated ADL or are temporarily prevented from surfacing does their heart rate fall below resting levels (Stephenson *et al.* 1986; Bevan *et al.* 1992). The heart rate data for the free-ranging South Georgian shag (Fig. 7) show certain similarities to those from tufted ducks performing 'extended' dives (dives in which the birds have to swim long horizontal distances under water to obtain their food; Stephenson *et al.*

1986). SGS1–3 show an initial reduction in heart rate followed by a slow rise, then, as dive duration increases, there is a further reduction. This temporal pattern is similar to that seen in tufted ducks.

The mean heart rate during diving was not significantly different from resting levels but was lower than levels for birds resting on the water channel (Table 4) and is probably lower than the heart rate while exercising at the surface (see Woakes and Butler, 1983). However, heart rates measured during the inter-dive period were similar to the elevated levels measured during flight. As a consequence, the mean heart rate measured over the dive cycle was significantly higher than the resting level, suggesting that these birds have an increased metabolic rate over the complete dive cycle. This feature was also found in the tufted duck (Bevan *et al.* 1992). The tufted duck has to work hard to overcome buoyancy in order to remain submerged, and it is therefore not surprising that these birds show an elevated dive cycle metabolic rate. Their cardiac output is, however, lower during diving than when working at a comparable rate at the surface. This reduction in cardiac output suggests that there is a lower blood flow to some tissues and organs during diving, although not to the working muscles (Bevan and Butler, 1992*b*).

The South Georgian shag is probably less buoyant than the tufted duck. The relative work required by the bird to remain submerged will therefore also be lower. At depth, buoyancy will be further reduced owing to the compression of the air-filled spaces between the feathers, which will again reduce the energy required to remain submerged. As the birds are active hunters, they will presumably be searching when at the seabed, which will require work to be performed by the active leg muscles. Any reduction in buoyancy will, therefore, reduce the total energy requirement and hence save the oxygen reserves.

Although the overall metabolic rate during a dive cycle is elevated, this does not preclude a reduction in metabolic rate during the portion of the dive when the birds are submerged. Indeed, the mean minimum heart rate of the South Georgian shags during diving was lower than the resting rate, which can be interpreted as a true 'diving bradycardia', which is indicative of a switch to anaerobic metabolism during submergence (Irving, 1939). Further evidence implying the use of anaerobic metabolism during diving is that the minimum heart rates recorded during diving in these free-ranging birds are similar to those found in forcibly submerged cormorants (Jones and Larigakis, 1988), a procedure that invokes severe vasoconstriction and anaerobiosis (Irving, 1939; Scholander, 1940; Butler and Jones, 1982). A gradual switch to anaerobic metabolism is also indicated by the progressive reduction in heart rate as a dive progresses.

That the estimated ADL is frequently exceeded by the South Georgian shag is well documented. However, the calculations of the ADL may be flawed. The variables used to calculate the ADL are (1) the usable oxygen stores in the body and (2) the rate at which these stores are used up. Neither of these variables has been measured in the South Georgian shag, but both can be estimated using data from other species. The ADL

of 120–150 s proposed by Croxall *et al.* (1991) used oxygen storage data obtained from penguins; unfortunately, they do not state how the rate of oxygen usage was calculated. Wanless *et al.* (1992) predicted an ADL of 174 s assuming the metabolic cost of diving to be only 1.5 times the standard metabolic rate (SMR), but suggested that the diving metabolic rate would be between 2 and 10 times SMR, which could shorten the ADL considerably (from 130 to 26 s). At a diving metabolic rate of 2.5 times the resting rate (the rate obtained from diving tufted ducks; Bevan *et al.* 1992), the ADL in the South Georgian shag would be less than 100 s and over 50 % of the dives made by the birds in the present study would have exceeded it.

At the point in the dive at which the ADL is reached, if the assumptions regarding the calculation of ADL are correct, then the animal has utilized all of the available oxygen. Even tissues such as the brain would then have to obtain their energy from a route other than oxidative metabolism. One possible solution is that, rather than making a dramatic switch to anaerobic metabolism at the ADL, the birds gradually increase the proportion of the energy requirement that is supplied by anaerobiosis *throughout the dive*. The body thus gradually conserves the remaining oxygen stores for the tissues that are oxygen-dependent. Evidence supporting this possibility could be inferred from the gradual reduction in heart rate that occurs as dive length increases.

Another possible solution is to decrease the overall metabolic rate as the dive progresses (Bevan *et al.* 1992). This could be achieved in a number of ways. First, as a shag dives deeper, the air spaces within its body and feathers will gradually be compressed, and its buoyancy and hence the amount of work required to dive will then be reduced (Stephenson, 1994). Second, we reported a reduction in abdominal temperature with dive duration. If changes in abdominal temperature reflect temperature changes occurring in other tissues, then the metabolic rate of these tissues will also fall, thus reducing the overall metabolic rate (see also Hill *et al.* 1987, for Weddell seals, *Leptonoychotes weddellii*). For example, if a tissue has a Q_{10} of 2, then a 10 °C change in temperature will cause a 50 % reduction in the metabolic rate of that tissue, a reduction in overall metabolic rate and thus an increase in the ADL. The most probable situation is that a combination of the mechanisms mentioned above is used and that the energy cost of diving is lower than the previously assumed values. Like Weddell seals, therefore, these birds may only infrequently exceed their true ADL.

The cause of the reduction in abdominal temperature during diving in free-ranging birds can only be speculated upon, but it is likely to be a combination of ingesting cold prey items (Grémillet and Plös, 1994) and the physical act of diving in cold water. The latter is particularly likely because of the high conductance and heat capacity of water, coupled with the reduced insulation of the body caused by compression of the feathers during a dive (Stephenson, 1994). Other studies have shown that diving animals lose heat during submergence (MacArthur, 1984; Hill *et al.* 1987; Bevan and Butler, 1992*a*; R. M. Bevan, P. J. Butler, A. J. Woakes, I. L. Boyd and J. P.

Croxall, unpublished data) although the temperature of the active muscles remains high through the generation of heat (Ponganis *et al.* 1993).

South Georgian shags have to elevate their metabolic rate to maintain their abdominal temperature when resting on water in a respirometer. This elevated metabolic rate is coupled with an increase in heart rate. High heart rates were also recorded at the end of every dive bout while the free-ranging South Georgian shags were on the water surface. These periods last for approximately 10 min, following which the abdominal temperature starts to rise. This elevated heart rate, which probably reflects an increase in metabolic rate, could be due to a number of factors: (1) the act of resting on cold water (Jenssen *et al.* 1989; Bevan and Butler, 1992a), (2) the activity associated with preening after a dive bout (the extra work generating heat), (3) the removal of anaerobic metabolites, and (4) specific dynamic action. Specific dynamic action, which is a byproduct of assimilating ingested food, could be an energetically inexpensive way of regenerating the heat lost through diving. It is clear that more research is needed on the effects of food intake on the thermoregulation of diving animals.

The fact that the South Georgian shag uses different groups of muscles for its two locomotory modes (swimming/diving and flying) may also help explain the apparent paradox between the estimated ADL and the recorded dive durations. The flight muscles are inactive during diving and, consequently, their demands on the oxygen stores will be restricted to, at most, a basal maintenance level which may be reduced even further if the temperature of these muscles is allowed to fall. Although not measured in this study, the flight muscle mass of the Phalacrocoracidae amounts to approximately 15–20% of the total body mass (Hartman, 1961). If the metabolic rate of this tissue is reduced, it would represent a considerable reduction in the overall metabolic rate. The actual tissues that are using the oxygen stores during a dive may, therefore, be only a relatively small fraction of the body mass and, even though these tissues are working at an elevated rate (Bevan and Butler, 1992b), the available oxygen stores may be sufficient for most dives to remain predominantly aerobic.

The recorded heart rates of South Georgian shags during flight were much lower than would be predicted from recent allometric equations (486 beats min⁻¹; Bishop and Butler, 1995). This may represent an adaptation of the cardiovascular system of the South Georgian shag to the dual roles of flying and diving through an increase in the cardiac stroke volume or an increased capacity of the tissues to extract oxygen from the blood.

This study shows how the physiology and behavioural ecology of the South Georgian shag are inextricably linked. It also raises some interesting questions about the control of the physiological processes employed by this free-ranging diving bird, particularly those mechanisms concerning thermoregulation and metabolism during submergence. It is likely that a number of mechanisms are employed by the South Georgian shag to increase the time that they are able to remain

submerged and therefore the time they have available for foraging. These mechanisms may also be used by other diving animals and may therefore assist in our interpretation of the physiology and behavioural ecology of diving birds and mammals in general.

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References

- ASHMOLE, N. P. (1971). Seabird ecology and the marine environment. In *Avian Biology*, vol. 1 (ed. D. S. Farner, J. R. King and K. C. Parkes), pp. 223–286. New York: Academic Press.
- BEVAN, R. M. AND BUTLER, P. J. (1992a). The effects of temperature on the oxygen consumption, heart rate and deep body temperature during diving in the tufted duck *Aythya fuligula*. *J. exp. Biol.* **163**, 139–151.
- BEVAN, R. M. AND BUTLER, P. J. (1992b). Cardiac output and blood flow distribution during swimming and voluntary diving of the tufted duck (*Aythya fuligula*). *J. exp. Biol.* **168**, 199–217.
- BEVAN, R. M., BUTLER, P. J., WOAKES, A. J. AND PRINCE, P. A. (1995a). The energy expenditure of free-ranging black-browed albatrosses. *Phil. Trans. R. Soc. Lond. B* **350**, 119–131.
- BEVAN, R. M., KEIJER, E. AND BUTLER, P. J. (1992). A method for controlling the feeding behaviour of aquatic birds: heart rate and oxygen consumption during dives of different duration. *J. exp. Biol.* **162**, 91–106.
- BEVAN, R. M., WOAKES, A. J., BUTLER, P. J. AND BOYD, I. L. (1994). The use of heart rate to estimate oxygen consumption of free-ranging black-browed albatrosses *Diomedea melanophrys*. *J. exp. Biol.* **193**, 119–137.
- BEVAN, R. M., WOAKES, A. J., BUTLER, P. J. AND CROXALL, J. P. (1995b). Heart rate and oxygen consumption of exercising gentoo penguins. *Physiol. Zool.* **68**, 855–877.
- BISHOP, C. M. AND BUTLER, P. J. (1995). Physiological modelling of oxygen consumption in birds during flight. *J. exp. Biol.* **198**, 2153–2163.
- BOYD, I. L. (1993). Selecting sampling frequency for measuring diving behaviour. *Mar. mammal. Sci.* **9**, 426–430.
- BUTLER, P. J. AND JONES, D. R. (1982). Comparative physiology of diving in vertebrates. In *Advances in Comparative Physiology and Biochemistry*, vol. 8 (ed. O. E. Lowenstein), pp. 179–364. New York: Academic Press.
- BUTLER, P. J. AND WOAKES, A. J. (1979). Changes in heart rate and respiratory frequency during natural behaviour of ducks, with particular reference to diving. *J. exp. Biol.* **79**, 283–300.
- CROXALL, J. P., NAITO, Y., KATO, A., ROTHERY, P. AND BRIGGS, D. R. (1991). Diving patterns and performance in the Antarctic blue-eyed shag *Phalacrocorax atriceps*. *J. Zool., Lond.* **225**, 177–199.
- FEDAK, M. A., PULLEN, M. P. AND KANWISHER, J. (1986). Circulatory responses of seals to periodic breathing: heart rate and breathing during exercise and diving in the laboratory and open sea. *Can. J. Zool.* **66**, 53–60.
- FURILLA, R. A. AND JONES, D. R. (1987). The relationship between dive and pre-dive heart rates in restrained and free dives by diving ducks. *J. exp. Biol.* **127**, 333–348.
- GENTRY, R. L. AND KOOYMAN, G. L. (1986). Methods of dive analysis. In *Fur Seals: Maternal Strategies on Land and Sea* (ed. R. L.

- Gentry and G. L. Kooyman), pp. 28–40. New Jersey: Princeton University Press.
- GRÉMILLET, J. H. AND PLÖS, A. L. (1994). The use of stomach temperature records for the calculation of daily food intake in cormorants. *J. exp. Biol.* **189**, 105–115.
- HARTMAN, F. A. (1961). Locomotor mechanisms of birds. *Smithson. misc. collns* **143**, 1–91.
- HILL, R. D., SCHNEIDER, R. C., LIGGINS, G. C., SCHUETTE, A. H., ELLIOTT, R. L., GUPPY, M., HOCHACHKA, P. W., QVIST, J., FALKE, K. J. AND ZAPOL, W. M. (1987). Heart rate and body temperature during free diving of Weddell seals. *Am. J. Physiol.* **253**, R344–R351.
- HOUSTON, A. I. AND CARBONNE, C. (1992). The optimal allocation of time during the diving cycle. *Behav. Ecol.* **3**, 255–265.
- IRVING, L. (1939). Respiration in diving mammals. *Physiol. Rev.* **19**, 112–134.
- JENSSEN, B. M., EKKER, M. AND BECH, C. (1989). Thermoregulation in winter-acclimatized common eiders (*Somateria mollissima*) in air and water. *Can. J. Zool.* **67**, 669–673.
- JONES, D. R. AND LARIGAKIS, S. (1988). The effect of breathing oxygen and air on diving bradycardia in cormorants (*Phalacrocorax auritus*). *J. exp. Biol.* **136**, 499–502.
- KOORYMAN, G. L., CASTELLINI, M. A., DAVIS, R. W. AND MAUE, R. A. (1983). Aerobic dive limits of immature Weddell seals. *J. comp. Physiol.* **151**, 171–174.
- KOORYMAN, G. L. AND PONGANIS, P. J. (1994). Emperor penguin oxygen consumption, heart rate and plasma lactate levels during graded swimming exercise. *J. exp. Biol.* **195**, 199–209.
- KOORYMAN, G. L., PONGANIS, P. J., CASTELLINI, M. A., PONGANIS, E. P., PONGANIS, K. V., THORSON, P. H., ECKERT, S. A. AND LEMAHO, Y. (1992). Heart rates and swim speeds of emperor penguins diving under sea ice. *J. exp. Biol.* **165**, 161–180.
- MACARTHUR, R. A. (1984). Aquatic thermoregulation in the muskrat (*Ondatra zibethicus*): energy demands of swimming and diving. *Can. J. Zool.* **62**, 241–248.
- MANGALAM, H. J. AND JONES, D. R. (1984). The effects of breathing different levels of O₂ and CO₂ on the diving response of ducks (*Anas platyrhynchos*) and cormorants (*Phalacrocorax auritus*). *J. comp. Physiol. B* **154**, 243–247.
- NICKERSON, D. M., FACEY, D. E. AND GROSSMAN, G. D. (1989). Estimating physiological thresholds with continuous two-phase regression. *Physiol. Zool.* **62**, 866–887.
- PONGANIS, P. J., KOORYMAN, G. L., CASTELLINI, M. A., PONGANIS, E. P. AND PONGANIS, K. V. (1993). Muscle temperature and swim velocity profiles during diving in a Weddell seal, *Leptonychotes weddelli*. *J. exp. Biol.* **183**, 341–348.
- SCHOLANDER, P. F. (1940). Experimental investigations on the respiratory function in diving mammals and birds. *Hvalradets Skrifter, Norske Videnskaps: Akad. Oslo* **22**, 1–131.
- STEPHENSON, R. (1994). Diving energetics in lesser scaup (*Aythya affinis*, Eyton). *J. exp. Biol.* **190**, 155–178.
- STEPHENSON, R., BUTLER, P. J. AND WOAKES, A. J. (1986). Diving behaviour and heart rate in tufted ducks (*Aythya fuligula*). *J. exp. Biol.* **126**, 341–359.
- STEPHENSON, R., HEDRICK, M. S. AND JONES, D. R. (1992). Cardiovascular responses to diving and involuntary submergence in the rhinoceros auklet (*Cerorhinca monocerata* Pallas). *Can. J. Zool.* **70**, 2303–2310.
- THOMPSON, D., HIBY, A. R. AND FEDAK, M. A. (1993). How fast should I swim? Behavioural implications of diving physiology. *Symp. zool. Soc. Lond.* **66**, 349–368.
- THOMSON, D. AND FEDAK, M. A. (1993). Cardiac responses of grey seals during diving at sea. *J. exp. Biol.* **174**, 139–164.
- WANLESS, S., HARRIS, M. P. AND MORRIS, J. A. (1992). Diving behaviour and diet of the blue-eyed shag at South Georgia. *Polar Biol.* **12**, 713–719.
- WILSON, R. P. AND WILSON, M-P. T. (1988). Foraging behaviour in four sympatric cormorants. *J. Anim. Ecol.* **57**, 943–955.
- WOAKES, A. J. AND BUTLER, P. J. (1975). An implantable transmitter for monitoring heart rate and respiratory frequency in diving ducks. *Biotelemetry* **2**, 153–160.
- WOAKES, A. J. AND BUTLER, P. J. (1983). Swimming and diving in tufted ducks, *Aythya fuligula*, with particular reference to heart rate and gas exchange. *J. exp. Biol.* **107**, 311–329.
- WOAKES, A. J., BUTLER, P. J. AND BEVAN, R. M. (1995). An implantable data logging system for heart rate and body temperature: its application to the estimation of field metabolic rates in Antarctic predators. *Med. Biol. Eng. comp.* **33**, 145–151.
- YDENBERG, R. C. AND CLARK, C. W. (1989). Aerobiosis and anaerobiosis during diving by western grebes: an optimal foraging approach. *J. theor. Biol.* **139**, 437–449.
- YEAGER, D. P. AND ULTSCH, G. R. (1989). Physiological regulation and confirmation: a BASIC program for the determination of critical points. *Physiol. Zool.* **62**, 888–907.
- ZAR, J. H. (1984). *Biostatistical Analysis*, 2nd edn. New Jersey: Prentice-Hall, Inc.