

A thorough and quantified method for classifying seabird diving behaviour

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Received: 24 April 2006 / Revised: 8 January 2007 / Accepted: 13 January 2007 / Published online: 5 April 2007
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Abstract Time-depth recorders are commonly deployed on diving animals to obtain information on their aquatic behaviour. The recorded data provide a 2D profile of diving activity. As analyses of diving behaviour from such profiles have become more complex, these analyses have often suffered from a lack of consistency and rigour. There is a growing need for a simple, comparative method to classify diving behaviour thoroughly and quantitatively. Here, a new approach to the classification of the dive profiles of penguins is described, which probably has applicability for many other diving predators as well. This simple approach uses a small, coherent set of criteria to classify behaviours in a detailed and quantified manner, and with relative objectivity. Classification of diving behaviour is possible from the temporal scale of a wiggle within a dive to the scale of a bout of dives. The new method will make comparisons between species

easier and clearer because these comparisons will be undertaken within a consistent, more objective framework.

Keywords Classification · Dive profile · Diving · King penguin · Penguin · Seabird

Introduction

Time-depth recorders are a commonly used technology for recording the diving behaviour of animals in the field. Data from such devices provide 2D dive profiles, which, although simplistic in their portrayal of the behaviour of diving animals functioning in a 3D environment (Mitani et al. 2004), nonetheless, provide a considerable amount of information. From 2D dive profiles, variables such as the depth, duration, and 2D shapes of dives can be ascertained. It is apparent from such data that there is a lot of variation in these factors within individual animals. This in turn suggests that many diving animals possess a repertoire of dives, which are likely to have different functions, placing an onus on accurately and consistently recognising different behaviours within dive profiles to aid in our understanding of the ecologies of diving species.

Consequently, there have been many attempts to categorise dives into different types based upon theorised functions. For example, Le Boeuf et al. (1988), Hindell et al. (1991), Wilson (1995), and Schreer and Testa (1996) recognise three fundamental dive types based on the shapes of dives: V, U, and W. This classification has been the basis for a multitude of studies on many avian and mammalian divers. However, it is apparent that, for seabirds at least, the present classi-

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fications employed are becoming insufficient for detailed analyses of diving behaviour. For example, the profiles of many dives can include a number of features that warp the shape of the profile. This can make classifications of dives by dive shape more complex (Schreer et al. 2001). Furthermore, to make full use of the large data sets now available on diving behaviour, it is rarely feasible to categorise dive data manually, i.e. dive by dive. Also, such comparisons based on visual assessment of dive profiles are subjective (Ropert-Coudert et al. 2000b; Lescroël and Bost 2005) and affected by reproducibility error (Schreer et al. 2001). Such studies fail to extract the maximum amount of information from expensive recording devices, intensive fieldwork, and impositions on study animals.

Thus, ways to identify and categorise diving behaviour objectively and in such a way that the process can be automated are clearly preferable. A number of studies from the diving mammal literature in particular have developed complex methods for categorising dives quantitatively, using, for example, artificial neural networks, shape-fitting algorithms, K-means clustering methods and discriminant function analysis (Lesage et al. 1999; see Schreer et al. 2001 and references therein). Yet, such methods require a high level of technical and/or statistical skill. There is a growing need for a simpler, yet thorough, method of quantitative classification that would be more accessible to many researchers.

The present paper describes a new overall approach to the classification of diving behaviours from the dive profiles of penguins. This method can classify diving behaviours from the scale of short-term behaviours within a dive to the diving bout. The methodology includes behavioural classifications, such as wiggles and dive shapes, which have been considered in previous studies, along with new classifications such as 'steps' in the dive profile and multiple, detailed metrics describing the bottom phase of the dive. The resulting classifications are, therefore, relevant with regards to penguins according to our present understanding of penguin behaviour and physiology. In turn, the behavioural classifications can form a detailed basis for analyses of other diving data (that could, for example, include temperature or acceleration data; Davis et al. 2001; Bevan et al. 2002), which will provide considerably more detail about the diving biology of these species. The behavioural classifications are achieved with a reasonable degree of objectivity by using a small, coherent set of criteria that can be readily automated.

The methodology of classification was developed using recently obtained data from a long-term eco-physiology study of the king penguin, *Aptendodytes*

patagonicus, and consultation with fellow seabird ecologists. Its applicability for use with multiple species has been tested using data from emperor penguins, *Aptenodytes forsteri*, gentoo penguins, *Papua pygoscelis*, and the Kerguelen shag, *Phalacrocorax verrucosus*. The value of this new approach is demonstrated through two concise examples of the potential uses of the classifications for exploring as yet unanswered questions about the diving biology of penguins. The examples centre on ecology and behavioural-physiology based topics concerning the king penguin. The authors intend to apply the methodology to data from further species of diving bird and, if possible, to some non-avian species as well, to ascertain the suitability of the methodology across a wide taxonomic range of diving homeotherms.

Materials and methods

Dive data were prepared and explored using purpose-written computer programs in Matlab (Version 6.0, The MathsWorks Inc., Natick, MA, USA). Matlab was also used to develop the programs to run the behavioural classifications of dive profiles. The data used in the development of these programs were obtained from fieldwork on male king penguins undertaken at the French station on Possession Island (46°25'S, 51°45'E), Crozet Archipelago during five austral summers spanning 2000–2005. Penguins were surgically implanted with loggers containing a pressure sensor with 8 or 12 bit sampling at 1 Hz. Details of the surgical procedures can be found in Froget et al. (2004) and Fahlman et al. (2005).

Final versions of the computer programs were used to classify the dive profiles of 14 king penguins representing around 200,000 dives, sampled with a pressure sensor resolution of <0.3 m. The programs were then tested on data available for emperor penguins (three birds, 10,553 dives), gentoo penguins (three birds, 1,709 dives), and Kerguelen shags (four birds, 682 dives), the latter two species being represented by individuals of two populations, one foraging in deep, open waters and the other in a shallow gulf. In light of these tests, further adjustments to the programmes were made to increase their flexibility and hence utility with multiple species.

Method to classify diving behaviour

A dive profile is a graphical representation of depth (y-axis) against time (x-axis). Periods when depth is at 0 represent time at the surface (the depth baseline) while values greater than 0 represent time underwater, i.e.

diving activity. The method for the classification of the behaviours in a dive profile described here, from behaviours within a dive through to the scale of a dive bout, uses a small, coherent set of criteria. These ensure a consistent classification of the behaviours. The criteria consist of:

1. Two defined trends that occur within the profile of dives (termed in the present study ‘wiggles’ and ‘steps’), which indicate clear changes in vertical velocity and appear as ripples in the profile (Figs. 1, 2). Wiggles and steps may well represent specific behaviours in themselves, such as incidence of feeding (e.g. Le Boeuf et al. 1988; Kirkwood and Robertson 1997; Roport-Coudert et al. 2000b, 2001) and/or, at least in the case of steps, changes in descent and ascent angles (e.g. Roport-Coudert et al. 2001; Sato et al. 2004). More specifically:
 - (a) Wiggles are a particular pattern in the dive profile over time during a dive where an increase in depth over time changes to a decrease in depth and then back to an increase in depth. This creates a short period in the dive profile that is concave in shape. Wiggles are defined as elements of the dive profile during which at three points the vertical speed passes below 0 ms^{-1} . (NB: If useful, certain wiggles could be ignored, e.g. using a threshold based on their depth range or duration.)
 - (b) Steps appear in a dive profile as a period of slowing of the descent or ascent of a dive. Steps are defined as periods within a dive during which vertical speed decreases to below a specific threshold value, $T_{\text{vert_vel}}$, but does not pass below 0 ms^{-1} . $T_{\text{vert_vel}}$ is set at 0.35 ms^{-1} for the king penguin. The travelling speed of a king

penguin underwater averages around 2 ms^{-1} (Sato et al. 2002) and vertical velocity tends to vary due to angle of descent rather than changes in swim speed (Bannasch 1995; Roport-Coudert et al. 2000b). Thus, steps tend to be periods when the bird is travelling close to horizontal as well being periods when vertical position in the water column is changing more slowly. With a body angle of 10° from horizontal, vertical velocity will be about 0.35 ms^{-1} and thus the definition of steps ensures that they will include periods of approximately horizontal movement. (Similarly to wiggles, certain steps could be ignored, e.g. based on depth of occurrence or depth range.)

The definitions for wiggles and steps ensure that they can be easily recognised by an automated system once vertical speed through a dive profile, i.e. change of depth over time, has been calculated (Fig. 1).

2. Several constants, each of which is based on a measure of a particular feature of diving behaviour, e.g. the maximum depth of a dive. These constants act as threshold values with which classifications of diving behaviour can be made, e.g. dives with a maximum depth greater than the threshold value might be classed as deep dives. There are two types of threshold value:
 - (a) Universal thresholds, the value of which remains the same regardless of the species of interest.
 - (b) Specific thresholds, which should be set with consideration of the species of interest. When classification is to be undertaken on a novel species, determination of these thresholds requires preliminary inspection of a sample of the dive profiles.

Fig. 1 Schematic of a step and a wiggle, which are both defined by specific changes in vertical speed within the dive profile (see text for details). The thin, grey, vertical lines represent the duration of the step and the wiggle while the thin horizontal lines represent their depth range. The thick grey, horizontal line represents the specific threshold value $T_{\text{vert_vel}}$

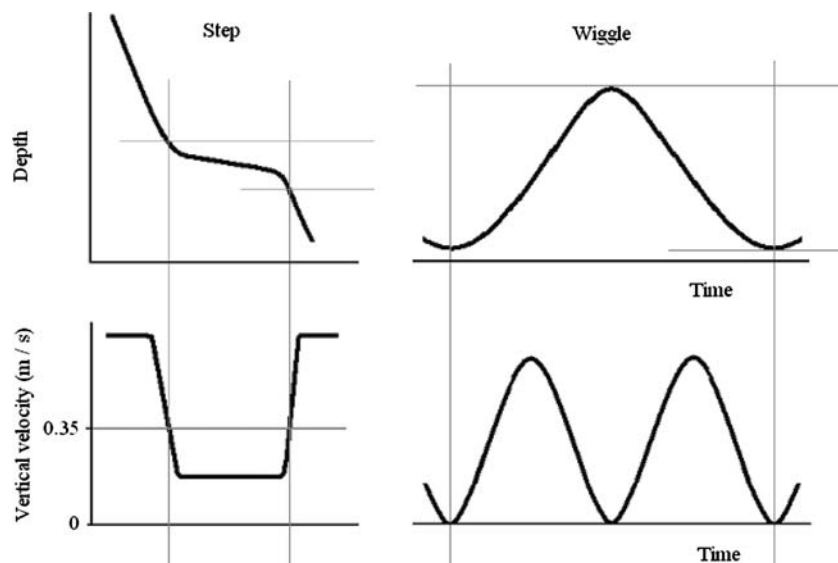
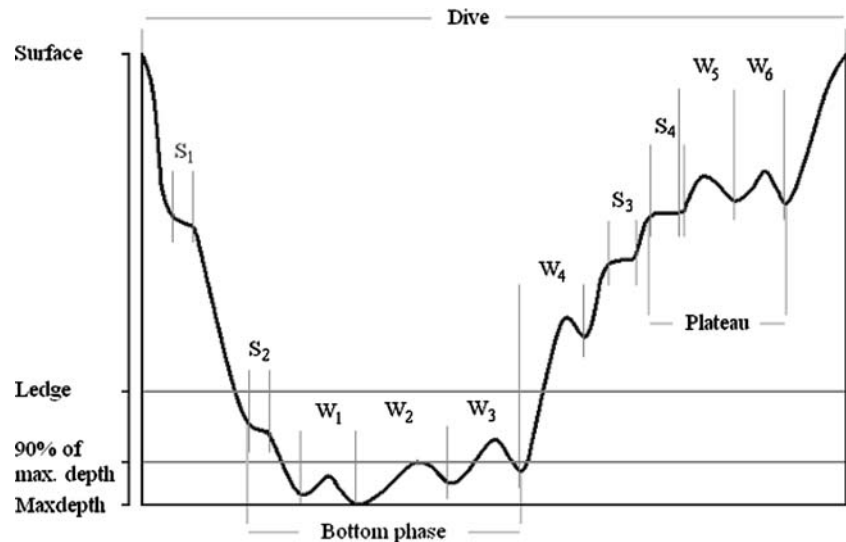


Fig. 2 Schematic of a dive, including the behavioural elements (steps and wiggles) and events (ledges and plateaus), that can be defined for analysis. S and W refer to steps and wiggles



Although not all thresholds used in the present methodology are discussed, for completeness, all are summarised in Table 1.

The threshold values used in the present methodology, such as maximum depth, or *Tvert_vel* included in the definition of steps, are necessarily arbitrary. However, in the case of universal thresholds, these values are justified having been chosen such that they generate useful classifications of diving behaviour from dive profiles. Where possible, they are based on values used by previous studies classifying diving behaviour. Furthermore, regardless of how they are derived, the constancy of the universal thresholds is valuable in enabling more direct and hence valid comparisons of diving behaviour between species. For specific thresholds, values should be set based on previous knowledge of the species and/or preliminary inspection of the raw data to be analysed. Throughout the remainder of the present paper, where specific thresholds are discussed, the value assigned to king penguins is given and justified.

It is important to note here a simple technique employed in the present paper to make analysis of behaviours within a dive easier. This was to firstly split the dive into two halves at the point of maximum depth and to then analyse the profile of each half of the dive from the surface downwards. Thus, vertical speed is always considered in the downward direction making the definitions of behaviours within the dive profile simpler to program and conceptually easier.

Measurement resolution

With any classification of diving behaviour, accuracy will be limited by the accuracy of the depth sensor, both in terms of sensory and temporal resolution, and by the

noise in the baseline of the data (Boyd 1994; Wilson et al. 1995). Indeed, in the present study, more adjustments to the classification programs were required in order that they could accommodate the variation in sensor resolution and baseline noise between data sets than the variation in diving behaviour between species. The temporary and sensory resolution of the depth data to be analysed represent, respectively, the duration of time between two successive data points and the minimum change in depth that can be recorded between two successive data points. Noise in the baseline is often due to wave action, hysteresis of the logger shell, recorder noise, and the influence of logger temperature on the pressure signal. Prior to dive analysis, the baseline must be cleaned. Thus, baselines with higher levels of noise reduce the minimum dive depth that can be interpreted as a dive (Green et al. 2005) and increase the inaccuracy in pinpointing the beginning and end of a dive. For example, analysis of a dive profile for an animal that dives with a vertical speed of 1.5 ms^{-1} , the data of which has a temporary resolution of 1 s and an uncertainty in the baseline of $\pm 2 \text{ m}$, could include absolute errors in dive duration greater than 5 s.

Consideration must also be given to the interplay among temporary resolution, sensory resolution, and *Tvert_vel*, and their affect on the number of successive data points over which behaviours within a dive can be searched for (*Tno_datapoints*). For example, to detect a step in the dive profile over three successive data points (e.g. *Tno_datapoints* = 3, as in the present study), the sensory resolution must be high enough such that the minimum measurable change in depth is less than the product of the sensory resolution and *Tvert_vel*. If this is not the case, the only solution is to increase *Tno_datapoints* as follows:

Table 1 The classification criteria, and threshold values derived from those criteria, used to define diving behaviours from 2D dive profiles (in conjunction with steps and wiggles)

| Behavioural parameter | Classification criteria and derived thresholds | | |
|---|--|------------------------------|-----------------------------------|
| | Classification criteria | Universal thresholds | Specific thresholds |
| Elements within a dive | | | |
| <i>Step</i> | No._datapoints Vert_vel | Tno._datapoints = 3 | Tvert_vel = 0.35 ms ⁻¹ |
| <i>Wiggle</i> | No._datapoints Vert_vel | Tno._datapoints | |
| Events within a dive | | | |
| <i>Ledge</i> | Max_depth | | Tledge_depth = 0.75 |
| <i>Plateau</i> | Max_depth | | Tledge_depth |
| | Dive_duration | Tduration = 0.1 | |
| | Depth_range | Tdepth_var = 0.1 | |
| Dives | | | |
| <i>Dive</i> | No._datapoints Max_depth | Tno._datapoints _b | Tmin_depth = 0 m ^a |
| | <i>Shallow dive</i> | Max_depth | Tdeep_depth = 50 m |
| <i>Deep dive</i> | Max_depth | | Tdeep_depth |
| Bottom | Max_depth | | Tledge_depth |
| V dive | Broadness index | | Tbroadness = 0.015 |
| u dive | | | Tbroadness |
| U dive | | | Tledge_depth |
| W dive | | | |
| Periods between dives within a bout | | | |
| <i>Inter-dive</i> | No._datapoints Max_depth | Tno._datapoints | Tmin_depth |
| | <i>Inter-dive duration 1</i> ^c | Max_depth | Tdeep_depth |
| <i>Inter-dive duration 2</i> ^d | | | |
| <i>Inter-dive duration 3</i> ^e | | | |
| Bout cycles (inter-bout period followed by a bout) | | | |
| <i>Bout</i> | Max_depth No._deep_dives | | Tdeep_depth |
| | No._dives | Tno._dives = 3 | |
| Deep sub- bout | Inter-dive duration 1 | | Tinter-dive_duration |
| Shallow sub-bout | Inter-dive duration 2 | | = 15 min |
| <i>Inter-bout period</i> | Max_depth | | Tdeep_depth |
| Travelling sub inter-bout period | No._dives Inter-dive duration 1 | Tno._dives | Tinter-dive_duration |
| Resting sub inter-bout period | Inter-dive duration 2 %time_submerged | T%time_submerged = 70 | |

The universal thresholds are applied to all species. The specific thresholds presented here are suitable for the king penguin and should be adjusted to suit the species of interest. All thresholds are constants

^a After baseline cleaning

^b Number of data points below the baseline

^c Total duration between two successive dives

^d Total duration between two deep dives

^e Surface duration between two deep dives

$$Tno_datapoints = 1 + [2 \times \text{sensory resolution} / (\text{temporal resolution} \times Tvert_vel)].$$

For example, if $Tvert_vel = 0.35 \text{ ms}^{-1}$, temporal resolution = 1 Hz and signal resolution $\pm 1 \text{ m}$, therefore $Tno_datapoints = 7$, i.e. the minimum number of data points over which vertical speed can be compared to $Tvert_vel$ is 7. Higher values of $Tno_datapoints$ result in the analysis reporting fewer steps and a longer mean duration of those steps.

Classifying phases of dives

In classifying dive phases, firstly, as is commonly done for analyses within dives (e.g. Le Boeuf et al. 1988; Wilson et al. 1996), the current methodology splits the dive into descent, bottom, and ascent phases. Once the start and end of the bottom phase is defined, then the definitions of the descent and ascent phases are simply the periods from the start of the dive to the start of the bottom phase and from the end of the bottom phase to the end of the dive, respectively. The present method-

ology starts by considering that the bottom phase is a period of the dive during which a relatively large number of feeding incidents may occur (this is often the case, e.g. in king penguins; Charrassin et al. 2002; Pütz and Chérel 2005). To define the start and end of the bottom phase, firstly a specific threshold is set, as a percentage of maximum depth below which wiggles and steps are then used to define the beginning and the end of the bottom phase (Tledge). It is below the depth of the ledge that the elements within the dive are used not only to classify the bottom phase of the dive but also the shape of the dive. The ledge is set at 75% of maximum depth for the king penguin since previous studies on this species have considered that the great majority of feeding incidents occur deeper than this (e.g. Charrassin et al. 2002) (Fig. 2). The bottom phase is defined as starting with the start of the first step or wiggle that occurs deeper than the ledge and ending with the end of the last step or wiggle that finishes deeper than the ledge.

The bottom phases of dives can be complex and highly variable and as such can demand detailed description. The classification of the bottom phase devised in the present study enables this (Fig. 3):

1. Broadness index; defined as:

- Bottom duration/dive duration.
- A higher number indicates a longer bottom duration relative to the duration of the entire dive and, therefore, a bottom period that appears less pointed.

2. Depth range index; defined as:

- Range in depth of the bottom phase/maximum depth.

3. Depth consistency index; defined as:

- Depth range index of dive₂ × (maximum depth of dive₂—maximum depth of dive₁)/maximum depth₂, where 1 denotes the previous deep dive and 2 denotes the deep dive of interest.
- Pairs of dives with small relative ranges in bottom phase depth and small relative differences in maximum depth, i.e. a high consistency in the nature of the deep part of the dive, will have lower index values, which can be indicative of benthic dives.

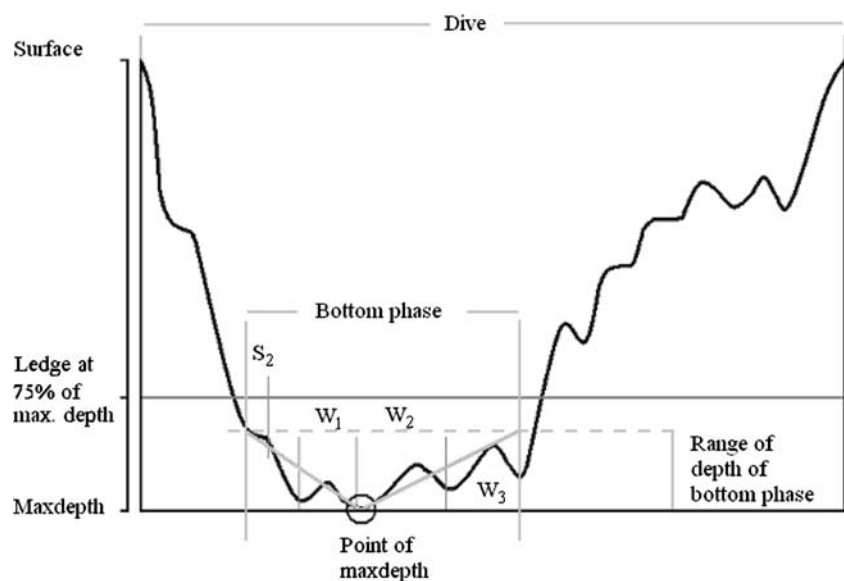
4. Symmetry index; defined as:

- Time into the bottom phase when maximum dive depth is reached/bottom duration.
- A value of 0.5 would indicate a ‘symmetrical’ bottom phase. A value close to 0 would indicate an asymmetrical bottom phase heavily skewed to the left and a value close to 1 an asymmetrical bottom phase heavily skewed to the right.

5. Degree of raggedness; defined as:

- Sum of the ranges in depth of the wiggles (i.e. their amplitudes; Fig. 1) during the bottom phase/duration of the bottom phase.
- Fluctuations in the dive profile during the bottom phase are recorded as wiggles (due to the definition of the latter). Bottom durations with the appearance of many fluctuations, particularly of high amplitude, are considered to be more ragged than smoother bottom durations.

Fig. 3 Schematic of a dive, considering the values calculated to describe the bottom phase. This description is made using indices of broadness, depth range, depth consistency, symmetry, and raggedness. S and W refer to steps and wiggles. The angled grey lines running from the point of maximum depth to the start and end points of the bottom phase shows the asymmetry of the bottom phase of the dive, described by the index of symmetry



Thus, a higher degree of raggedness indicates a greater number of wiggles during the bottom phase and/or greater changes in depth associated with those wiggles. Note that the degree of raggedness is also the mean vertical speed during the bottom phase.

Finally, plateaus are events within dives that are relatively long and horizontal, and may have a particular function (Ropert-Coudert et al. 2000b). In the present classification, they occur specifically during either the first part of the descent phase or the latter part of the ascent phase, i.e. at a depth shallower than the ledge (Fig. 2). They are defined as composing of one or more wiggles and/or steps, they exist for more than 10% of the duration of the entire dive (i.e. a universal threshold derived from the dive duration) and have an overall variation in depth of less than 10% of the maximum dive depth (a universal threshold derived from maximum dive depth). These values for the two universal thresholds ensure that events classified as plateaus indeed appear as plateau-like when observed in a dive profile. Further, events classified as plateaus are thus not short-term ripples in the dive profile that are either unlikely to be of importance, or represent a different, shorter-term phenomenon.

Classifying dive shape

Based on dive shape classifications of previous studies, four shapes of dive are distinguished (V, u, U, and W) (Figs. 4–7). In the present study, however, classification by dive shape is undertaken according to the shape *only of the bottom phase of the dive*. Thus, these classifications are made independently of the shapes in the dive profile during the descent and ascent phases, which are perhaps most noticeably affected by the presence or otherwise of plateaus. Furthermore, the threshold values set to define each shape, for the present data, have been chosen empirically after visual inspection of samples of the data, such that each dive is classified with a shape that most represents the general shape of the bottom phase.

Dives that do not include any wiggles or steps below the ledge, by definition, do not have a bottom phase. These dives are classed as V dives (Fig. 4). All other dives that include wiggles and/or steps below the ledge, therefore, include a bottom phase. Their shape is defined from the numbers and positions of steps and wiggles in this phase, coupled with the broadness index of the bottom phase:

- V dives (other than those without a bottom phase) are any dive where the bottom phase has a

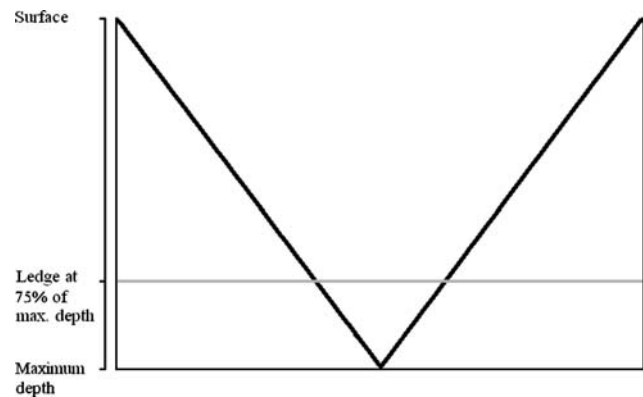


Fig. 4 Schematic of a V shaped dive, including the ledge of the dive. This V dive does not have any wiggles or steps and hence has the most V-like shape possible

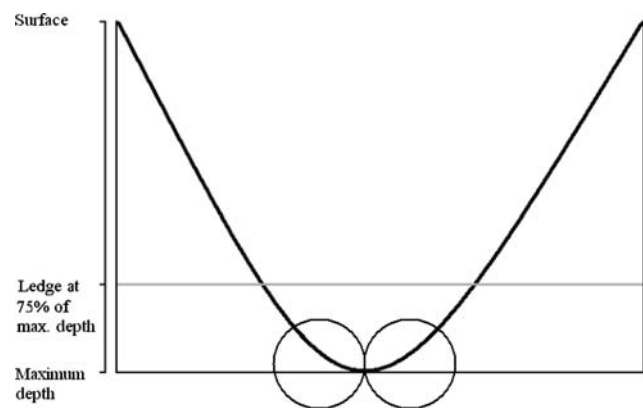


Fig. 5 Schematic of a u shaped dive, including the ledge of the dive. The entirety of the two steps defining this dive shape are circled

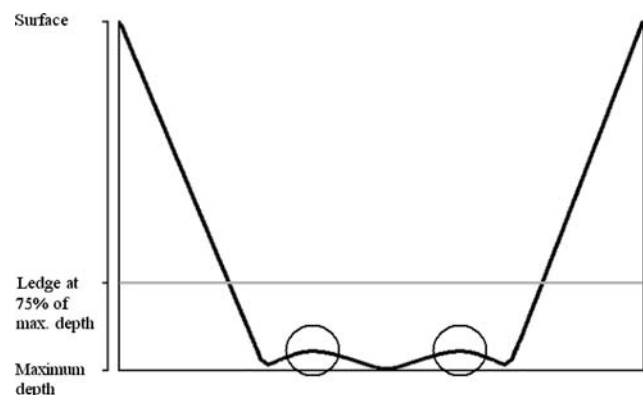


Fig. 6 Schematic of a U shaped dive, including the ledge of the dive. The apexes of the two wiggles always present at the 'corners' of these dives, defining the dive shape, are circled

broadness index of less than a threshold value (0.015 for king penguins).

All dives with a broadness index >0.015 are u, U, or W dives:

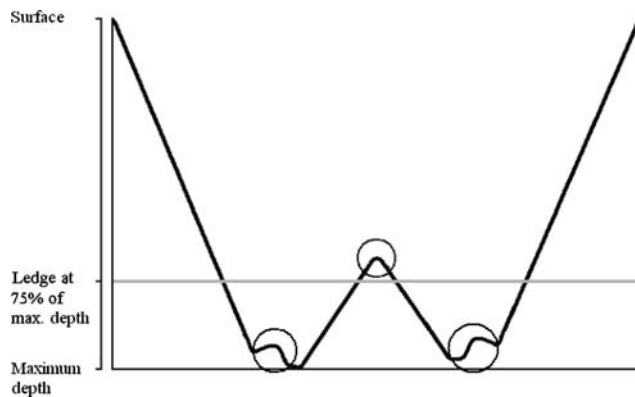


Fig. 7 Schematic of a W shaped dive, including the ledge of the dive. The entirety of the two wiggles always present at the 'corners' of these dives, and the apex of the wiggle that reaches above the ledge, are *circled*. These are used to define the dive shape

- u dives are relatively smooth dives with a fairly consistent change in vertical speed throughout the bottom phase of the dive (Fig. 5). They can include wiggles and steps above the ledge, however, they always include just two steps below the ledge and no wiggles. These steps are towards the bottom of the dive at the two points either side of maximum depth where the velocity of the bird decreases below T_{vert_vel} .
- U dives always include at least two wiggles due to the 'corners' of the dive within the bottom portion of the dive (Fig. 6).
- W dives are special cases of U dives. One or more wiggles occur that are between at least two others, i.e. between at least the wiggles representing the 'corners' of the dive, and have a minimum depth that is

less than the ledge of the dive. Thus, a central portion of the bottom phase of W dives is at a considerably shallower depth than maximum depth (Fig. 7).

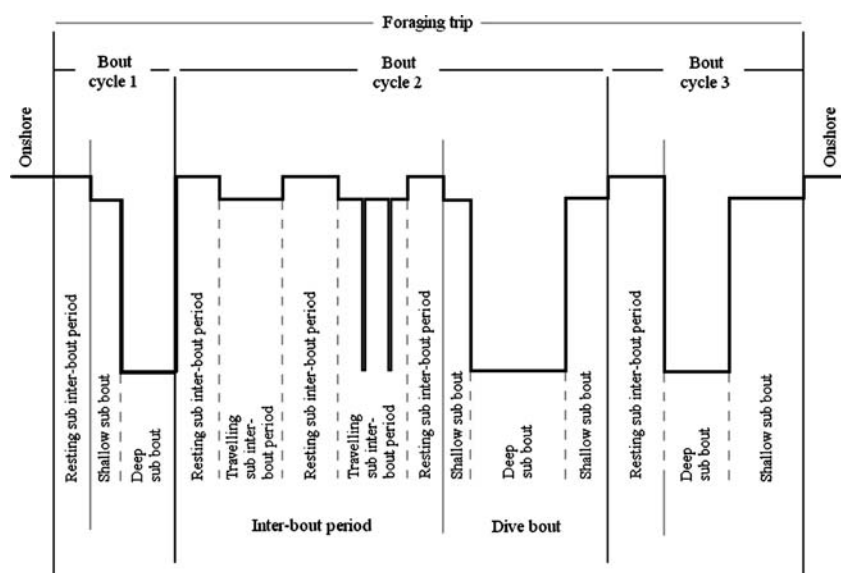
Beyond the shape, the broadness index, the number of steps, and the number of wiggles, the bottom phase of the dive can be described further by assigning the indices of depth range, depth consistency, and asymmetry. For U and W dives, the degree of raggedness can also be calculated.

Classifying cycles of diving bouts

While penguins tend to perform the majority of their dives in discrete series termed dive bouts, nevertheless the combinations of dive types within bouts is highly variable. Penguins also undertake a number of dives in isolation or at least not obviously within a coherent series of dives. Thus, it is overly simplistic to attempt to categorise diving bouts as periods of diving activity and inter-bout periods as periods of cessation from diving activity. However, although diving behaviour at the level of the foraging trip is complex, with the present method this scale of behaviour is classified simply and effectively.

Three threshold values (one universal and two specific) are sufficient to define dive bouts, periods between dive bouts (inter-bout periods), and discrete periods of activity within both dive bouts and inter-bout periods (subbout periods and subinter-bout periods, respectively, Fig. 8). The universal threshold is for the minimum number of dives within a bout or subbout, set at 3. The two specific thresholds are the maximum duration at the surface between two dives within a bout,

Fig. 8 Schematic of a foraging trip undertaken by a king penguin. The trip consists of three bout cycles. The dive profile is shown in *black* and emboldened



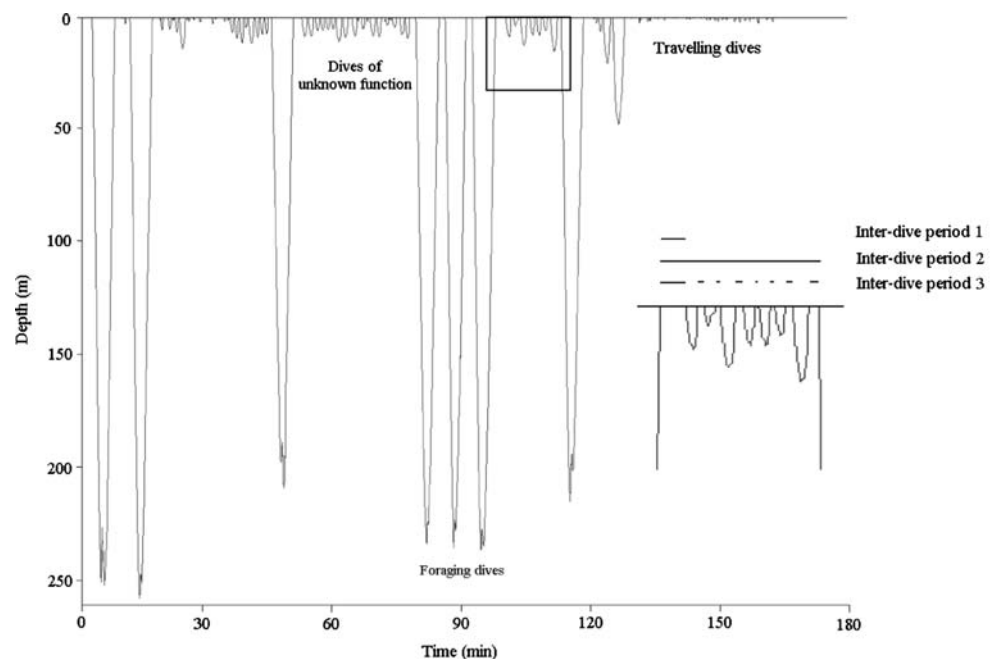
i.e. the maximum duration of the inter-dive period (Tinter-dive_duration, 15 min for the king penguin ensures that bouts generally include more than just a few dives) and the depth below which a dive is classified as deep (Tdeep_depth; 50 m for the king penguin based on data from Charrassin et al. 2002). Due to the importance of the value assigned to Tdeep_depth in the definition of dive bouts, we suggest the use of a method that is as objective as possible to determine this value for the species of interest. For example, frequency plots of maximum depth from diving data for penguins often show bimodality, interpreted as indicating the ranges of shallow, travelling dives, and of deep, foraging dives (e.g. Kooyman et al. 1992; Green et al. 2005). For successive deep dives, a comprehensive set of definitions is required for the inter-dive period between them because these periods often include shallow dives. In the present methodology, the inter-dive period between deep dives can be considered in terms of: (1) the duration at the surface until the next dive, whatever the depth (inter-dive period 1), (2) the total duration until the next deep dive (inter-dive period 2), and (3) the total duration spent at the surface until the next deep dive (inter-dive period 3; Fig. 9).

The presence of a diving bout is initially recognised by at least three successive deep dives (Boyd et al. 1994) with less than Tinter-dive_duration between each successive one, i.e. inter-dive period 2 is less than Tinter-dive_duration. The end of this set of deep dives occurs, therefore, when inter-dive period 2 is greater than Tinter-dive_duration. Then, the presence of a set of

shallow dives immediately following the deep dives is defined by shallow dives that are three or more in number and with durations between them that are less than Tinter-dive_duration. Finally, the presence of a set of shallow dives immediately before the deep dives is defined likewise. The set of deep dives is thus a subbout of deep dives, while the sets of shallow dives are each subbouts of shallow dives. Together, these subbouts form a diving bout (Fig. 8). However, it is of course possible to have a subbout of deep dives that is not preceded and/or followed by a bout of shallow dives. Furthermore, by definition, it is possible to have single or paired deep dives within subbouts of shallow dives, and many shallow dives within subbouts of deep dives.

Next, each diving bout is linked with the previous inter-bout period (to form a 'bout cycle'). The reason for this order is that it is usually the case that a foraging trip ends with a subbout of deep dives followed by a subbout of shallow dives (e.g. Pütz et al. 1998) i.e. thus ends with the finish of a diving bout. Inter-bout periods rarely represent periods of complete cessation from diving. Rather, they often include sets of shallow dives and/or isolated deep dives. These dives can constitute a noteworthy proportion of the entire inter-bout period. It is thus likely to be useful to subcategorise inter-bout periods depending upon the amount of diving activity that occurs, e.g. as either resting or travelling subinter-bout periods. To achieve this, subinter-bout periods are firstly designated as those that include more than three successive dives with an inter-dive period 1 between them of less than Tinter-dive_duration (either shallow

Fig. 9 Typical dive profile of a king penguin diving during a foraging trip. The boxed area is shown enlarged as an inset. Refer to the text for further details



dives only or including sparse deep dives of either one or two in series), and those that do not. Having split up the inter-bout period this way, each of these subinter-bout periods are defined as travelling or resting depending upon whether more or less than 70% of the period is spent submerged. Although necessarily arbitrary, the value of 70% is considered reasonable since it is considerably greater than 50%, the latter value indicating that an equal amount of time is spent submerged and resting. Thus, the former value represents a threshold beyond which a clear majority of the time is spent underwater, presumably in the form of travelling dives.

In summary, bout cycles are categorised into dive bouts and inter-bout periods. The former include a subbout of deep dives and can also include subbouts of shallow dives before and/or after the deep subbout. Inter-bout periods consist of resting subinter-bout periods and/or travelling subinter-bout periods.

Discussion

Previous classifications of penguin diving behaviour

Maximum dive depth was the first metric of diving behaviour recorded by time depth recorders (Schlander 1940; Kooyman 1966; Kooyman et al. 1971). It is probably for these reasons that maximum dive depth was the first variable used to classify dives (e.g. Williams et al. 1992; e.g. Chappell et al. 1993). Maximum depth was also employed in the current study to classify subbouts into shallow and deep subbouts. However, beyond simple classifications, maximum depth is not an effective criterion with which to classify dives, despite its ease of use. This is in part because the depth of dives can show strong diel variation, e.g. due to prey migration in the water column (Wilson et al. 1993; Bost et al. 2002). Thus, dives at different times of the day can have very different maximum depths (Schreer et al. 2001). Classification of dive shape is a logical progression from depth classification since shape provides information about what animals are doing during dives. Furthermore, while maximum depth may vary through the day, dive shape can remain the same (Schreer et al. 2001).

A number of studies have classified penguin dives by shape (e.g. Wilson 1990, 1995; Kirkwood and Robertson 1997; Ropert-Coudert et al. 2000b). In particular, shape categorisation has been applied to foraging dives in an attempt to understand different hunting strategies. For example, Wilson (1995) identified U and W shape dives, with prey pursuit occurring predominantly during ascent in U dives and during the bottom phase in W dives (Pütz and Cherel 2005). V shape dives were

considered as purely exploratory dives, though they may have a number of other functions such as predator avoidance (Schreer et al. 2001). Many studies of diving in penguins have based their classifications of the dive profile on the classification of Wilson et al. (1995), e.g. Williams et al. (1992), Chappell et al. (1993), Wilson et al. (1996), Kirkwood and Robertson (1997), Pütz et al. (1998), Lescroël and Bost (2005), Ropert-Coudert et al. (2000b), Ropert-Coudert et al. (2002), and Pütz and Cherel (2005). In some cases, certain studies focusing on particular species have added further categories of dive to the classification of Wilson (1995). For instance, Lescroël and Bost (2005), who recorded data on gentoo penguins, *Pygoscelis papua*, added aspects of classifications from Le Boeuf et al. (1988) and Williams et al. (1992) to those of Wilson (1995) to produce six dive shapes for gentoo penguins, including U shaped benthic feeding dives and asymmetrical feeding dives.

Advantages of the new method of classification

Because the dive profiles of penguins are rarely smooth or conform to a dive shape, the majority of researchers have classified dive shape by visual inspection (e.g. Tremblay and Cherel 2000; Pütz and Cherel 2005; Lescroël and Bost 2005). However, this is extremely time consuming and subjective (Schreer et al. 2001). Furthermore, the logic of the classifications themselves is problematic. Perhaps the biggest difficulty is that the classifications are not mutually exclusive. For example, dives with plateaus were considered as a separate shape category of dive by Ropert-Coudert et al. (2000b); however, such dives can also have a variety of overall shapes. While some classifications incorporate 'asymmetrical dives' as dive shapes (e.g. Lescroël and Bost 2005), V dives can be asymmetrical if descent and ascent rates are not equal.

With the present methodology, once the relevant thresholds have been set, classification of the shape of each dive in a data set is not undertaken manually by visual inspection or by using complex procedures such as the application of shape-finding algorithms (e.g. Schreer et al. 2001). Nor does it require additional data over and above the dive profile such as swimming speed (Lesage et al. 1999). Instead, simply wiggles and steps (i.e. specific changes in vertical velocity), along with two threshold values based on the ledge and the broadness index, are used to define dive shape, with each shape category being mutually exclusive. Wiggles and steps are also used for recognising plateaus. Thus in the present method, a shape, the presence or otherwise of plateaus, and the phase(s) within which

those plateaus occur, are assigned to each dive based on quantified criteria. Consequently, shape classification is not affected by deviations in the dive profile within the dive above the ledge, making the classification more robust, yet the details of these deviations are still assigned to each dive.

Previously, the bottom phase of a dive has often been recognised simply as the part of the dive greater than a certain percentage of maximum depth. For example, for king penguins, this value has been set at 90% (Charrassin et al. 2002) or 85% (Pütz and Cherel 2005). For emperor penguins, 85% has also been used (Kirkwood and Robertson 1997; Wienecke et al. 2007). However, such definitions are limited in that if the bottom period of a foraging dive is considered to be the main period of feeding (Ydenberg and Clark 1989), and functionally different to the predominantly travelling phases of the descent and ascent periods, then the deepest, e.g. 15% of the dive may not incorporate all of this period, or alternatively include more than just this period (Charrassin et al. 2001). In the present methodology, the bottom phase starts and ends with a step or wiggle, the first and last below a threshold level that is set conservatively, i.e. shallowly. This definition of the bottom phase is thus flexible to changes in the depths of dives during which the majority of feeding incidents may occur.

Furthermore, there can be many variations within the bottom phase of a dive that cannot be satisfactorily accounted for simply by creating more dive shape categories (e.g. Lescroël and Bost 2005). For example, certain studies have noticed that some dives appear to have much more ragged bottom phases than others and have added such dives as a dive ‘shape’ accordingly (e.g. Bost et al. 2007). However, with the new method of classification, this feature of the dive can be assigned over and above the shape of the dive. Furthermore, while the definition of the bottom phase generally used by previous studies means that the start and end of the bottom phase is at the same depth, in fact many dives exhibit a slope upwards or downwards during the deepest part of the dive. This is accounted for in the new method of classification by the indices of depth range and symmetry of the bottom phase. These indices may be especially relevant in consideration of the distribution of prey at depth. A further important use for the level of detail by which bottom phases are classified in the present methodology is in recognising possible benthic dives by species such as gentoo and emperor penguins (Rodary et al. 2000). Successive dives with horizontal bottom phases spanning a similar range of depth, i.e. with a low index of depth range,

and which consistently reach a similar maximum depth, are a good indication of benthic diving. This aspect of dives is measured by the index of depth consistency. This index is similar to, but more powerful than, the ‘intra-depth zone’ devised by Tremblay and Cherel (2000) for determining the presence of benthic diving, because the index of depth consistency is a continuous variable and includes more factors to describe benthic dives.

Thus in total, with the present method, each dive is defined not only by shape, but is also then assigned information about the quantity, location, and type of elements and events within the dive (wiggles, steps, and plateaus) and the detailed nature of the bottom phase. A considerable amount of detail is therefore provided to characterise each dive.

At the level of the dive bout, dive analysis can be potentially complex and has been attempted by very few studies of penguins (Mori 1997). Dive bouts consisting of different proportions of different dive types and shapes, and in different sequences (cf. Kooyman et al. 1992; Pütz et al. 1998), may well represent functionally different behaviours (Lesage et al. 1999). For example, periods that include shallow dives often occur at the end of foraging trips, as the animal returns to shore (Pütz et al. 1998). Inter-bout periods including both shallow dives and isolated deep dives are most common near the start of foraging trips, as the animal travels from the shoreline out into the sea towards foraging areas, and presumably periodically makes exploratory dives in search of a food patch (Wilson 1995; Pütz et al. 1998). Dives can also sometimes occur alone, or in pairs, or as mixtures of deep and shallow dives (Pütz et al. 1998).

Thus, categorising dive bouts purely as periods when dives occur in quick succession limits the detail of diving analyses at the diving bout level. Furthermore, several authors have pointed out the need for an objective method to determine bout end criteria (see Boyd et al. 1994; Mori 1997). However, while broken stick models can provide such objectivity, they have been developed to describe sequences of simple, homogeneous behaviour and thus have limited suitability for grouping dives into diving bouts (Boyd et al. 1994). It is also important to define subbouts and subinter-bouts. The new method of classification extends to the scale of the diving bout, using just three constants to make the classification quantified, repeatable, and easily automated. Furthermore, it provides a considerable amount of information about the nature of dive bouts that is likely to be useful for analyses of broad scale diving behaviour and physiology.

Applying the methodology

Below, we briefly consider two examples that showcase the applicability of the present method of classification for analysing, in detail, the diving behaviour of king penguins.

Behavioural physiology after a deep dive

Once the dive profile has been classified accurately and in detail, there is considerable power in the 2D dive profile alone for discovering more about the diving behaviour and also the physiology of a species. For example, accurate descriptions of the periods between deep dives, as is used in the present method of classification for describing dive bouts, may well prove central in uncovering the benefit to king penguins of the diving patterns regularly exhibited during these times (Fig. 9). In the present data, and in other unpublished data on king penguins (Butler, Handrich, Halsey, and Fahlman), it can be seen that after a number of minutes subsequent to the end of a deep dive, king penguins often undertake a short series of shallower dives usually with a maximum depth of at least 10 m and sometimes 20 m or more. Given that travelling dives are probably most energetic and time efficient when the descent and ascent phases are minimised and therefore will be very shallow (Wilson 1995), it seems unlikely that the function of the aforementioned, medium depth dives is, at least solely, for travelling. Thus, presently, their function is unclear.

It is as yet unknown whether king penguins are able to undertake deep foraging dives without incurring an increase in lactate within the body, or indeed an accumulation of nitrogen. However, in the emperor penguin, the congeneric of the king penguin, post-dive lactate concentration in the blood can be considerably higher than resting levels after very long dives (Ponganis et al. 1997). Thus in king penguins, a series of medium depth dives after a foraging dive may represent a period of exercise to oxidise lactate (Butler 2004) accumulated during the deep dives (Kooyman et al. 1992; Kooyman and Ponganis 1998). Using the present classifications, it will be possible to test this hypothesis by investigating the relationships between the depths and durations, and possibly also the shapes, of deep dives, against the durations of the three definitions of the inter-dive period.

The ecology of the dive

Detailed analysis of dive profiles using the present methodology can provide important behavioural

information with which to base the analysis of other measurements recorded concurrently. For example, while the present method of classification can recognise two types of deviation within the dive profile, wiggles and steps, as yet it is unknown whether they represent different behaviours. Although wiggles are considered to indicate feeding attempts (e.g. Bost et al. 2007), it is unclear whether steps are also feeding attempts, possibly of a different type. Furthermore, it may be the case that, for example, steps during the descent phase of a dive have a different function to steps during the ascent phase of a dive. According to oesophageal temperature data, the majority of feeding episodes by king penguins occur during the bottom and ascent phases of the dive (Bost et al. 2007). Thus, steps during the ascent phase may be feeding episodes while steps during the descent phase may, for example, predominantly represent avoidance behaviour, perhaps as a reaction to a perceived threat of predation. With more information on the locations of feeding episodes within a dive from, for example, beak opening data (Wilson et al. 2002) and from more detailed analyses of oesophageal temperature data (Ropert-Coudert et al. 2000a; Bost et al. 2007), the functions of wiggles and steps from different phases of the dive will be resolved. This may well prove to be an important step in furthering our understanding of the feeding ecology of king penguins.

Conclusions

A detailed, quantified and relatively objective classification of diving behaviour at the scales of the diving bout, the dive and elements and events within the dive is necessary if we are to glean all the information available from 2D profiles of dives. The new method of classification, which provides such detail, shows promise for enabling further investigation into the ecological and physiological aspects of diving behaviour. While the examples given to demonstrate the potential of applying the present method are based on king penguin data, the method also runs effectively with data recorded for two other penguin species and a species of shag, by adjusting the specific threshold values to tailor the analysis for the species of interest. An important finding arising from the application of the methodology to multiple species is that in each case, only two threshold values were changed. This is despite the four species encompassing a range of body masses from 1.7 to 35 kg, a range of maximum dive depths from 20 to 374 m and of maximum dive durations from 175 to 985 s. Therefore, we are confident that the new method will work effectively on many other diving species. The

threshold values that were changed were the maximum duration at the surface between two dives within a bout (Tinter-dive_duration) and the depth below which a dive is classified as deep (Tdeep_depth). Interestingly, during some dive bouts by emperor penguins, there was no value of Tdeep_depth that distinguished foraging dives from non-foraging dives, because wiggles were apparent in dives with a maximum depth of only 1 or 2 m. It is likely that these dives represent foraging dives under pack ice (Kooyman and Kooyman 1995; Wie-necke et al. 2007).

The present paper and associated computer programs were developed in response to the need for a clear yet relatively simple, detailed, quantified and automated approach to classifying diving behaviour from dive profiles. The result is a new method of classification that makes comparisons between species easier and clearer because these comparisons are made within a consistent, reasonably objective framework. This will allow, for example, comparative measures between populations and species, elucidating unifying patterns and theorems. It is hoped that other researchers also using time-depth recorders will at least make use of some of the ideas presented here and that, in turn, some standardisation of the analysis of dive profiles will develop. Dr. Yves Handrich, the author of the computer programmes used in the present study, has the intention to further develop his programs for use with as wide a range of species as possible. As such, Dr. Handrich would be interested in receiving data sets, initially for single, typical animals, of any diving species for which there is an interest in utilising the method of dive classification detailed in the present paper.

Acknowledgments The data reported on king penguins were collected and analysed during a study supported by IPEV Programme 394. We thank three referees for their in-depth and informative comments on earlier versions of this manuscript.

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