Dive Bout Organization in the Chinstrap Penguin at Seal Island, Antarctica

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Abstract — Diving behavior of 2 breeding Chinstrap penguins (*Pygoscelis antarctica*) was studied focusing first and primarily on dive bouts rather than dives themselves. Analysis of dive bout organization revealed (1) though there are differences between solitary dives and dive bouts in dive duration and dive depth, the first dives of dive bouts do not differ from solitary dives in the dive parameters, (2) mean dive duration during bout correlates positively to both mean dive depth during bout and mean surface interval during bout, while number of dives during bout negatively correlates to both cost (consumed energy) and duration of a dive cycle during bout. These findings suggest the following possibilities on foraging behavior of penguins: (1) their decision to repeat diving depends on the result of the first dive at a site, and the first dives of bouts would tend to be searching or evaluating dives though they would be also successful foraging dives, (2) they repeat diving at a foraging patch until foraging efficiency decrease to a threshold of diminishing returns.

The diving behavior of penguins has been studied with the help of recording devices. Previous studies have focused on the description of maximum diving depth or number of dives to defined depths (Kooyman et al. 1982, Lishman & Croxall 1983, Kooyman & Croll 1987, Croxall et al. 1988). However, devices which can record diving behavior continuously or nearly continuously have been developed recently, and provide information on other diving chacters such as duration, timing and profiles (e.g. Naito et al. 1990, Williams et al. 1992, Kooyman et al. 1992, Watanuki et al. 1993, Bengtson et al. 1993, Chappell et al. 1993a, b). These studies have shown that dives often occur in discrete bouts and that diving behavior is under the influence of foraging conditions such as food availability or daily vertical migration of prey. However, to date few detailed analysis of the dive bouts have been carried out because of the lack of method to determine objective bout ending criteria (BEC; if a dive interval between 2 dives is longer than this criterion, each dive belongs to a different bout) in a satisfactory way.

Sibly et al. (1990) developed a log frequency analysis to determine BEC objectively. The diving behavior of Chinstrap penguins recorded continuously at Seal Island (South Shetland Islands) in 1987 was reported in Bengtson et al. (1993), but dive bouts were not described. Using diving data recorded continuously by time-depth recorders (TDRs), I report here the primary analysis of dive bout organization (rather than dives themselves) performed by 2 Chinstrap penguins (*Pygoscelis antarctica*) breeding at Seal Island in 1991. BEC were determined by log frequency analysis.

Methods

The study was conducted at Seal Island, the South Shetland Islands, Antarctica (60°59.5'S, 55°24.5'W) from late December, 1990 to mid-January, 1991. Time-depth recorders (TDRs) used in the study were TDR-20S (Yanagikeiki Co., Ltd.), which record diving behavior continuously by scratching a recording tape with a

stylus. The TDR is 2.5 cm dia. $\times$ 9 cm length and weighs 80 g in air (34.5 g in seawater) with the battery. The TDRs used in this study record dives $\geq$ 1 m in depth and $\geq$ 0.3 min in duration. Thus, shallow and short dives in quick succession, which are likely to be traveling/porpoising dives, do not record perfectly (Williams et al. 1992). Further details of TDRs are found in Naito et al. (1990). TDRs were attached to the feathers of the middle of the backs of breeding Chinstrap penguins with quick-setting epoxy glue and 2 plastic cable ties between 27-30 December, 1990. Each bird with a TDR had 2 eggs at the time of attachment. Chicks hatched between 31 December, 1990 and 2 January 1991. In total, 15 TDRs were attached to penguins and the recorders were recovered from the birds between 17-18 January, 1991. Three TDRs were not recovered because of nest abandonment and 10 other TDRs did not work well (the depth meters functioned well but timers did not). The 2 TDRs which recorded diving behavior perfectly were obtained from 2 birds, which were named C9005 and C9014, respectively. Recording periods were 21 days for C9005 and 19 days for C9014. Stomach contents were sampled by stomach flushing (Wilson 1984) the instrumented birds at the time of recovery.

Continuous diving records on recording tapes were enlarged and digitized as in Naito et al. (1990). The diving data recorded during the incubating period were excluded from analysis. During incubation, birds do not have to return with prey to feed chicks, and this affects the number of dives and/or each dive duration.

To distinguish between dives that are associated with foraging and dives that involve traveling, short and shallow dives less than 20 s or 5 m were excluded. These criteria are based on Bengtson et al. (1993). Thus, most of analyzed dives in this study are considered dives associated with foraging, whether they were successful or not.

Penguins perform a number of dives in relatively quick succession and the groupings of these dives are called dive bouts. To estimate BEC for each individual, surface intervals were plotted in log frequency and fitted into the Poisson two random processes model (Sibly et al. 1990, Martin & Bateson 1993). A two random processes model using calculated BEC fitted the data well, since R^2 were large (0.902 and 0.881). The calculated BEC values also yielded a small number of misassigned dives (32 of 1087 dives for C9005 and 27 of 1550 dives for C9014, respectively).

Parameters of dives and dive bouts were then calculated for individuals according to each individual BEC. Surface intervals longer than 3 h were excluded on estimating BEC and further analysis on dive bout interval because they are likely to be time on land. The longest surface interval within 3 h was 2.2 h for C9005 and 2.5 h for C9014, while the shortest surface interval within the range over 3 h was 14 h for C9005 and 15.7 h for C9014. Estimation of cost (consumed energy) during dive cycle (dive duration plus surface interval) was based on Culik and Wilson (1991) and Culik et al. (1991) (metabolic rate for swimming is $10-16$ W·kg^{-1} and metabolic rate during surface interval is 9.32 W·kg^{-1}).

Results

During the measurement period, 1089 and 1636 dives for 13 and 11 foraging trips were recorded from the 2 penguins (C9005 and C9014, respectively). Only 2 of 1089 dives (0.2%, C9005) and 86 of 1636 dives (5.2%, C9014) were less than 5 m in depth or 20 s in duration. These dives were excluded from subsequent analysis. Calculated BEC were 5.4 min for C9005 and 9.4 min for C9014. On the basis of each BEC those dives were split into 90 and 77 dive bouts, respectively. Twenty-nine dive bouts of 90 (32.2%) for C9005 and 11 dive bouts of 77 (14.3%) for C9014 were composed of only 1 dive ("solitary" dives). The statistical summary of dives and dive bouts are shown in Tables 1 and 2. C9005 dove for significantly shorter period but to greater depths and tended to stay on the surface slightly shorter than C9014 (U-test, p<0.01, p<0.01 and p=0.052, respectively). C9005, whose BEC value was small, performed significantly shorter dive bouts (smaller number of dives during bout) than C9014 (U-test, p<0.01) and also had shorter inter-dive

Table 1. Diving behaviors performed by each bird. Values are mean±SD. Range and sample size are in parentheses. Differences between individuals were examined by U-test and significant level is indicated by *p>0.05 or **p<0.01.

	C9005	C9014	Individual difference
Sex	M	M	
BEC (min)	5.4	9.6	
Body mass (kg)	3.1	3.6	
Dive duration (min)	1.56±0.38	1.61±0.37	**
	(0.5–2.9, N=1087)	(0.5–2.6, N=1550)	
Dive depth (m)	46.6±20.0	27.6±14.4	**
	(5.0–110.7, N=1087)	(5.0–76.4, N=1550)	
Surface interval	1.0±0.8	1.2±1.4	p=0.052
shorter than BEC (min)	(0.3–5.3, N=993)	(0.3–9.3, N=1556)	
Number of dives	83.7±49.9	148.7±65.8	**
per foraging trip	(17–227, N=13)	(28–273, N=11)	

Table 2. Summary of dive bout statistics for each bird. Values are mean±SD. Range and sample size are in parentheses. Statistical comparisons between individuals were examined by U-test and significant levels are indicated by *, p<0.05 or **, p<0.01.

	Solitary dives	C9005	C9014	Individual difference
Number of dives	included	12.1±16.7	21.2±24.2	**
during bout		(1–84, N=90)	(1–90, N=77)	
	excluded	17.4±18.0	24.3±24.6	NS
		(2–84, N=61)	(2–90, N=66)	
Inter-dive bout	included	23.7±23.6	34.1±29.3	**
duration (min)		(6.0–130, N=77)	(10.2±149, N=66)	
	excluded	34.7±31.8	35.2±30.5	NS
		(6.0–130, N=48)	(10.2–149, N=55)	
Number of dive bouts	included	7.5±5.0	7.4±3.3	NS
per foraging trip		(1–16, N=13)	(1–9, N=11)	
	excluded	4.7±2.8	6.4±2.8	p=0.07
		(1–11, N=13)	(1–12, N=11)	

bout durations (U-test, p<0.01), including solitary dives. These differences are, however, partly due to the large number of solitary dives by C9005. Statistically significant differences were found between solitary dives and dive bouts in mean dive duration during bout and mean dive depth during bout for both birds (Table 3). There were no statistical differences between solitary dives and dive bouts in pre-dive nor post-dive bout intervals.

First dives of dive bouts were significantly shorter than the mean duration of other dives within the same bout (Wilcoxon signed-rank test, 1.54±0.34 and 1.68±0.32 min for C9005, p<0.01 and 1.49±0.52 and 1.66±0.27 min for C9014, p<0.01) although their durations were

correlated positively (r=0.58, p<0.01 for C9005 and r=0.62, p<0.01 for C9014, respectively), while second dives of dive bout did not differ from other dives within the bout (Wilcoxon signed-rank test, 1.75±0.40 and 1.64±0.31 min, p>0.1 for C9005, and 1.65±0.41 and 1.64±0.27 min, p>0.1 for C9014). The first dives were also shallower than mean depth of other dives within the same bout (Wilcoxon signed-rank test, 39.1±17.7 and 53.4±18.6 m, p<0.01 for C9005 and 24.3±16.3 and 30.5±13.3 m, p<0.01 for C9014) although the depths correlated positively (r=0.73, p<0.01 for C9005 and r=0.50, p<0.01 for C9014, respectively). Second dives of bouts did not differ from other dives during the bout (Wilcoxon

Table 3. Statistics summary of solitary dives and dive bouts parameters for each bird. Values are mean±SD. Range and samples size are in parentheses. Statistical comparisons between solitary dives and dive bouts are examined by U-test and significant levels are indicated by *, $p < 0.05$ or **, $p < 0.01$. Pre-dive and post-dive intervals for including solitary dives are described in Table 2 as inter-dive bout duration.

	Including solitary dives	Solitary dives	Dive bouts	Statistical differences
C9005				
Mean dive duration during bout (min)	1.60±0.36 (0.5–2.2 N=90)	1.48±0.44 (0.5–2.2 N=29)	1.66±0.30 (0.9–2.2 N=61)	**
Mean dive depth during bout (m)	46.9±18.4 (6.2–90.9 N=90)	36.8±15.4 (6.2–68.1 N=11)	51.7±17.8 (10.7–90.9 N=61)	**
Pre-dive bout interval (min)	–	16.9±11.5 (6.1–61.0 N=27)	27.7±27.7 (6.0–130 N=49)	NS
Post-dive bout interval (min)	–	18.0±16.2 (7.1–78.4 N=24)	26.3±26.0 (6.0–130 N=53)	NS
C9014				
Mean dive duration during bout (min)	1.60±0.34 (0.8–2.4 N=77)	1.39±0.45 (0.9–2.1 N=11)	1.66±0.32 (0.8–2.4 N=66)	**
Mean dive depth during bout (m)	27.6±14.2 (5.0–53.6 N=77)	16.8±15.7 (5.0–53.3 N=11)	29.4±18.0 (5.0–70.3 N=66)	**
Pre-dive bout interval (min)	–	25.5±14.0 (12.3–47.6 N=5)	33.2±30.1 (10.2–149 N=64)	NS
Post-dive bout interval (min)	–	16.4±6.3 (10.2–28.4 N=9)	35.4±30.5 (10.2–149 N=57)	NS

Table 4. Correlation coefficients between mean dive parameters during bout, excluding solitary dives. Significant level is indicated by *, $p < 0.05$ or **, $p < 0.01$. Sample sizes are N=61 for C9005 and N=66 for C9014.

Bird	Dive duration vs Dive depth	Dive duration vs Surface interval	Dive duration vs Number of dives	Dive depth vs Number of dives	Cost[a] per dive cycle vs Number of dives	Cost[b] per dive cycle vs Number of dives	Dive cycle duration vs Number of dives
C9005	0.88**	0.25*	–0.33**	–0.27*	–0.34**	–0.35**	–0.33**
C9014	0.87**	0.34**	–0.24*	–0.29*	–0.29**	–0.29**	–0.33**

a: swimming metabolic rate=10W/kg, b: 16W/kg

signed-rank test, 49.5±20.9 and 51.0±18.4 m, $p > 0.1$ for C9005 and 29.8±15.8 and 29.6±12.8 m, $p > 0.1$ for C9014).

Those first dives did not differ from solitary dives which were shorter and shallower than dives in bouts (duration: 1.48±0.44 and 1.54±0.34 min, U-test $p > 0.1$ for C9005 and 1.39±0.45 and 1.49±0.52 min, U-test $p > 0.1$ for C9014, depth: 36.8±15.4 and 39.1±17.7 m, U-test $p > 0.1$ and 16.8±15.7 and 24.3±16.3 m, U-test $p > 0.1$ for C9014).

Table 4 shows correlations between dive bout parameters (excluding solitary dives). Mean dive duration during bout correlated positively to mean dive depth during bout and mean sur-

face interval during bout in both birds. Number of dives during bout correlated negatively to both mean dive duration during bout and mean dive depth during bout in both birds. Consequently, it negatively correlated to mean dive cycle duration during bout, which was calculated as total dive bout duration divided by number of dives during bout or inverse of dive frequency during bout. Number of dives during bout also negatively correlated to mean cost per dive cycle (total dive bout cost divided by number of dives during bout). Neither pre-dive bout interval nor post-dive bout interval related to other dive bout parameters.

Discussion

Diving behavior

In a previous study (Bengtson et al. 1993), mean dive duration and mean dive depth recorded by penguins at Seal Island in 1988 were 1.3 min and 35.9 m. In this study, recorded mean dive duration and mean dive depth in 1991 were 1.6 min and 27.6–46.6 m. These results are consistent with the previous study. Mean dive depth performed by 2 birds were 27.6 m and 46.6 m and these values correspond closely to the depth at which krill was the most abundant around Seal Island in early January 1991 (30–40 m, Japanese Fishery Agency 1993). The birds in this study fed on almost exclusively krill (*Euphausia superba*). Thus dive depth is assumed to reflect foraging conditions, namely vertical distribution of prey (see also Bengtson et al. 1993 or Croxall et al. 1985). The individual difference of dive depth might be due to differences in foraging areas. Diurnal patterns are not likely to be responsible for this because diurnal patterns did not seem to differ between individuals. Foraging range of penguins in Seal Island in early January is estimated to be 7–28 km (Bengtson et al. 1993, Japanese Fishery Agency 1993). Thus, it is not strange that individuals breeding in the same colony may forage in different areas.

Organization of dive bouts

The birds studied fed on krill, a patchily distributed prey. Although it is impossible to exactly distinguish successful and unsuccessful foraging dives, solitary dives should be considered primarily as unsuccessful and/or searching and/or evaluating behaviors because dives should be successive for efficient foraging if prey is found (even if patch size is small). It is interesting that the first dives of bouts are significantly shorter and shallower than mean duration and mean depth of other dives later in the bout, and that they do not differ from solitary dives. These findings indicate that the first dives of bouts are similar to searching and/or evaluating dives even if they are successful foraging dives. It seems that the decision to repeat diving

depends on the result of the first dive at a site and that the first dives of bouts are consequently for searching and/or evaluating as well as successful foraging dives.

Correlations between mean dive duration and mean dive depth during bout and between mean dive duration and mean surface interval during bout are reported by Chappell et al. (1993a) in Adelie penguins, but they do not report on number of dives during bout. Number of dives during bout is a specific characteristic for dive bout analysis. There are 4 possible explanations about how the birds decide how many times to repeat diving and when to stop diving. (1) They repeat diving until they become full, (2) they repeat diving until prey runs out completely, (3) they repeat diving until they approach physiological limits and (4) they repeat diving until foraging efficiency becomes too low, or they stop diving when prey density decreases to a very low level. These possibilities are not necessarily exclusive.

The first possibility may apply to the last dive bouts of some foraging trips. This seems to be consistent with the negative correlation between mean dive duration during bout and number of dives during bout because their product would correspond to the total amount of prey catch. However, more than 1 dive bout usually occurs in a foraging trip, so the first explanation is not the best one.

The second possibility would be applicable to cases in which number of dives during bout is small. However, it is hardly possible that the largest krill patch encountered by the birds during the study period would have been depleted after less than 100 dives. The highest krill density detected by echo sounder was more than 500 g/m^2 around Seal Island in early January, 1991 (Japanese Fishery Agency 1993). Thus, the second possibility is also an unlikely explanation. Other explanations are needed for dive bouts with a large number of dives.

The third possibility is consistent with the negative relationships between number of dives during bout and both cost per dive cycle during bout and dive cycle duration during bout. This possibility is presented on diving behavior of thick-billed murres by Croll et al. (1993), in which they consider lactic acid produced during

long anaerobic dives as accumulated exhaustion. Estimated aerobic diving limit (ADL, Kooyman 1989) of Chinstrap penguins is 0.9 – 1.7 min based on the following assumptions; O_2 storage is the same as in the congener Adelie penguin (43 – 51 ml/kg, Kooyman & Davis 1987, Chappell et al. 1993a) and swimming metabolic rate is 10 – 16 W/kg (Culik et al. 1991, Culik & Wilson 1991). Mean dive duration performed by the birds was 1.6 min. If ADL is 0.9 min anaerobic metabolic duration is 0.7 min. It seems probable that the surface intervals, 1.0 min for C9005 and 1.2 min for C9014, are too short to reduce produced lactate completely during the surface interval. But if ADL is 1.7 min, the value exceeds mean dive duration. Even if partial dive cost is supplied anaerobically, anaerobic metabolic duration seems to be so short that most of the produced lactate would be reduced during the surface interval. As it is difficult to estimate the ADL exactly, this possibility seems partly likely but shall be investigated further.

The fourth possibility is based on optimal foraging theory (see Stephens & Krebs 1986 for review). In case of foraging on patchily distributed prey, total amount of prey catch increases but increasing rate (foraging efficiency) decreases as foraging time increases. In such a case, the animal using the patch should leave the patch when the foraging efficiency reaches a marginal value of maximum foraging efficiency. As a basic unit of foraging behavior for penguins is a dive cycle, penguins repeating dive cycles at a foraging patch should stop the dive cycles and leave the patch when the net energy gain per a dive cycle decreases to this marginal value. If the number of dives during bout indicates the number of dives for optimal prey patch use, the optimal number of dives during bout is expected to decrease when the cost of dive cycle increases, because the number of repeating times of dive cycle at which the marginal value is given becomes smaller. This predicts the negative correlation between cost per dive cycle and number of dives during bout, and this correlation is found in the study (Table 4). The cost per dive cycle is influenced by durations of diving and surface interval and underwater ratio per dive cycle (diving duration: surface inter-val). In this study, dive duration correlates to surface interval positively (Table 4). This suggests that underwater ratio per dive cycle does not change widely and that the cause of change of the cost per dive cycle might not be change of ratio but change of dive cycle duration. Negative correlation between number of dives during bout and dive cycle duration is found in the study (Table 4), and this correlation is consistent with the prediction from optimal foraging theory. This discussion assumes that the birds have information about prey distribution such as mean distance between prey patches and mean prey density at a patch. It seems probable that the birds had general information on prey distribution around the breeding colony at which they had been staying for over a month before the study period began, though this is difficult to prove. Positive relationship between mean dive duration during bout and mean surface interval during bout supports the assumption that the birds forage optimally (Kramer 1987, Houston & Carbone 1992). Thus, this possibility seems to be the most likely one, though it is necessary to investigate both prey distribution and physiological condition of penguins for quantitative predictions and further testing.

Organization of dive bout is affected by not only foraging condition but also physiological restrictions in air-breathing animals. Further investigation is needed to clarify how these factors function to affect organization of dive bouts.

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