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RESEARCH

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Hydrodynamic handicaps and organizational complexity in the foraging behavior of two free-ranging penguin species

Xavier Meyer[1,2*†], Andrew J J MacIntosh[3,4†], Akiko Kato[1,2], André Chiaradia[5] and Yan Ropert-Coudert[1,2]

Abstract

Background: Animal movement exhibits self-similarity across a range of both spatial and temporal scales reminiscent of statistical fractals. Stressors are known to induce changes in these statistical patterns of behavior, although the direction and interpretation of such changes are not always clear. We examined whether the imposition of known hydrodynamic disruptors, bio-logging devices and flipper bands, induces changes in the temporal organization (complexity) of foraging sequences in two penguin species, little penguins (*Eudyptula minor*) and Adélie penguins (*Pygoscelis adeliae*).

Results: Detrended fluctuation analysis showed that foraging sequences produced by little penguins carrying larger loggers were more complex, i.e., were more erratic tending toward greater stochasticity, than those carrying smaller loggers. However, logger size did not affect complexity in foraging sequences of Adélie penguins. Logger position was associated only weakly with altered complexity in little penguins, with individuals carrying loggers in the middle of their backs displaying slightly more complex dive sequences than those carrying loggers lower on their backs. Finally, despite their known negative effects on penguin fitness, flipper bands were not associated with dive sequence complexity in little penguins.

Conclusions: Despite that externally attached devices can disrupt certain behavioral parameters in diving seabirds, we found mixed evidence in support of the hypothesis that such devices significantly disrupt the time-structured organizational properties of foraging sequences in the two penguin species investigated. However, smaller species carrying larger loggers, and perhaps those positioned higher on their backs, may experience an added element of noise in their behavioral sequences that may indicate a departure from foraging behavior observed under normal, unburdened conditions.

Keywords: Fractal analysis, Behavioral complexity, Adélie penguin, Little penguin, Flipper band, Bio-logger, Hydrodynamic handicap

Background

Fractal patterns are found everywhere in nature, e.g., in the shapes of clouds, mountains and coastlines, or in plant structures such as those produced in the Romanesco broccoli (*Brassica oleracea* var. *botrytis*) [1]. Such patterns are also known to emerge in spatial and temporal sequences of animal movement, which exhibits self-similarity across a range of measurement scales [2–7]. Three approaches have used fractal geometry in the field of animal movement ecology: (1) measuring step length distributions (sensu the Lévy flight foraging hypothesis) [5, 8–11], (2) spatial fractal dimension estimation [12–16], and (3) fractal time series analysis of behavior sequences [17, 18]. These studies highlight how highly irregular patterns of behavior may reflect an optimal strategy to facilitate resource encounters in heterogeneous environments.

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Fractal time series analyses of animal behavior measure the structure of behavior as it occurs through time, which is linked to the concept of behavioral organization [17, 19]. Borrowing from the field of complexity science, such studies have adopted the term 'complexity' to refer to the correlation structure of the time series, which behave as nonlinear systems [20]. Complexity in diverse biological phenomena is considered to be adaptive because it is error-tolerant, making it possible to buffer changes arising from both intrinsic (e.g., reproductive state and hormones) and extrinsic factors (e.g., environmental perturbations) [21]. On a temporal scale, physiological or behavioral changes can impact the complexity observed in time series data collected from diverse systems [18]. These deviations from normal behavioral patterns in nonlinear systems, known as 'complexity loss', were first observed in physiological systems producing heart rate variability [22], stride patterns [23] and neural activity [24]: pathological systems produce times series with altered complexity signatures. Complexity loss has now also been observed in various forms of animal behavior, such as not only foraging and movement but also vigilance, postural behavior and even social behavior, when animals are confronted with some or another stressor [6, 25–30]. For example, Spanish ibex (*Capra pyrenaica*, [25]) and Japanese macaques (*Macaca fuscata*, [6]) infected by parasites have showed a decrease in behavioral sequence complexity. Similarly, Adélie penguins (*Pygoscelis adeliae*, [30]) treated with corticosterone implants also exhibited reduced dive sequence complexity in comparison with untreated (control) birds. Moreover, Indo-Pacific bottlenose dolphins (*Tursiops aduncus*, [29]) exposed to the presence of motor boats also showed a decrease in the complexity of their dive sequences. Thus, complexity loss, as far as it has been detected in altered behavior sequences, is predicted to reduce an animal's fitness long term.

Altered complexity signatures may reflect changes toward either greater stereotypy or greater randomness, depending on the nature of the disruption [17, 18, 26]. Kembro et al. [31] for instance showed increased stochasticity in the movement behavior of mosquito larvae exposed to lethal and sub-lethal doses of essential oils. Similarly, greater stochasticity was also observed by Rutherford et al. [26] in behavioral patterns of hens exposed to novel housing conditions. The contrasting responses to the presence of stressors appear to depend on the specific type of stressor faced by individuals, with greater stochasticity expected in cases of acute stress and greater stereotypy expected in cases of chronic stress [18, 27]. The concept of complexity loss was thus extended to allow for the fact that changes in both directions can equate to suboptimal complexity signatures, as both reflect a departure from optimal patterns of behavioral organization that can be detrimental over the long term [18]. We could easily hypothesize about the potential benefits of increased complexity in the vigilance behavior of animals exposed to novel environments in which the location of potential resources, but also potential threats, cannot be a priori known. However, we would predict a return to normal, i.e., more deterministic behavior patterns over time, as animals familiarize with their surroundings, whereas the same might not be said of an animal exposed to a truly chronic stressor.

Here, we re-examined published datasets that found an effect of either external devices [32, 33] or flipper bands [34] on the foraging activities of penguins to determine whether hydrodynamic handicaps can induce altered complexity signatures in foraging (diving) sequences of two species of penguin: the Adélie penguin and the little penguin (*Eudyptula minor*). Indeed, previous studies of Adélie and little penguins have revealed short-term impacts of back-attached diving recorders on diving activities through comparisons of diving parameters in groups of birds equipped with devices of different sizes [32, 33]. These experiments offer a good framework to test whether the attachment of such devices, which imposes a known hydrodynamic handicap [34, 35], would also induce organizational changes in patterns of foraging behavior. Thus, we predicted the existence of variation in the organizational complexity of foraging behavior in relation to logger size (large vs small loggers) and logger position (higher vs lower on the penguin's back). Since large loggers and those positioned higher on the back should increase drag relative to smaller loggers and those positioned lower on the back [34, 35], we assumed that the organizational properties of foraging sequences in birds under the latter conditions were more similar to those in birds under unburdened, control conditions. Following the results of Fallow et al. [36], predictions about the impact of flipper bands should differ between short-term (acute stressor) and long-term (chronic stressor) attachment experiments on little penguins. Thus, we predicted short-term effects on the organizational properties of foraging sequences but not long-term effects.

Methods

We studied little penguins from the Penguin Parade colony at Phillip Island, Victoria, Australia (38°30′S, 145°09′E) and Adélie penguins in Dumont d'Urville, Adélie Land (66°39′S, 140°00′E).

Little penguins

Studies were conducted on 15 males and 16 females from 9 to 26 November 2004 (logger size and position experiment) and 21 females between November and December

2005 (Flipper band experiment). In both cases, all birds were in the guard stage, raising 1 or 2 chicks. Further details on the colony and field protocol can be found in [32] and [36].

The effects of different logger sizes and positions of attachment were investigated using large and small loggers placed higher or lower on the backs of birds. Large loggers were cylindrical, two-channel depth data loggers (62 mm × 18 mm, 17 g, LTD 1, 200–100, Lotek, Canada) accounting for ca. 4.9% of the cross-sectional area of little penguins, while small loggers were cylindrical (53 mm x 15 mm, 17 g, M190-D2GT, Little Leonardo, Japan) accounting for ca. 3.4% of the cross-sectional area of little penguins. All loggers sampled depth once per second with a 0.1 m accuracy. Large and small devices were attached either to the lower (recommended to minimize drag [35]) or middle back of the birds (where we expected the loggers to increase drag). The experimental design included four groups: birds with either small ($n = 21$) or large loggers ($n = 15$), placed either near the tail ($n = 17$) or in the middle ($n = 19$) of the back (See details in [32]). Birds were monitored for a single trip at sea during the guard phase. All trips lasted one day only. Ropert-Coudert et al. [32] showed that birds carrying large loggers had shorter dives that were more frequent than penguins carrying small loggers. Logger position had no statistical effect on little penguin diving behavior.

The experiment testing the effect of flipper bands was conducted using three groups of individuals: an unbanded control group ($n = 7$), a banded control group ($n = 6$) that had been carrying bands for a number of years, and a treatment group of unbanded birds that were temporarily banded specifically for this experiment ($n = 7$). Short-term effects (days) were examined in the treatment group by comparing the diving data from a first foraging trip when birds were not banded with the diving data obtained during the next foraging trip when birds had been banded. In parallel, long-term effects (years) were examined by comparing the diving data of the banded control group with the diving data of the unbanded control group. Diving activity was monitored using the M190-D2GT data loggers described above (see details in [36]). Fallow et al. [36] showed that birds in the treatment group dived deeper, longer, descended slower and ascended quicker with longer surface times after dives when banded but no long-term effect was found.

Adélie penguins

The study was conducted on 14 birds from 18 December 2001 to 4 January 2002 during the guard phase. A logger size effect was investigated using two sizes of loggers: large loggers were cylindrical, 3-channel W200-PDT loggers (102 × 22 mm, 50 g, Little Leonardo, Tokyo, Japan) which measured speed and depth at 1 Hz and accounted for 1.4% of the cross-sectional area of Adélie penguins ($n = 7$); small loggers were M190-D2GT loggers described above, which recorded depth at 1 Hz and acceleration at 16 Hz, and accounted for 0.8% of the cross-sectional area of Adélie penguins ($n = 7$). Diving data and swim speed (either measured directly via an anteriorly mounted propeller or reconstructed based on diving angle and depth changes) of two groups measured over a single foraging trip of 2–3 days were compared (see details in [33]).

Data analysis

Following the analytical approach described in MacIntosh et al. [37], we used detrended fluctuation analysis (DFA) to measure long-range dependence as an index of temporal complexity in penguin diving sequences. DFA was developed by Peng et al. [38] to provide a more robust estimate of the Hurst exponent, which measures the degree to which time series are long-range dependent and statistically self-affine. The scaling exponent calculated by DFA (α_{DFA}) measures the slope of the line on a double logarithmic plot of average fluctuation as a function of scale [39, 40] and is bound to (0, 1) for fractional Gaussian noises (fGn) and (1, 2) for fractional Brownian motions (fBm) [41, 42]. Values in the range (0.5, 1) and (1.5, 2) reflect persistence while those in the range (0, 0.5) and (1, 1.5) reflect antipersistence in the time series for fGn and fBm, respectively, with 0.5 and 1.5 reflecting randomness (white noise). Theoretically, α_{DFA} is inversely related to the fractal dimension, which represents an index of structural complexity [1]. Since its introduction, DFA has become widely used in a diverse array of biological systems (e.g., [22, 24, 43]), including animal behavior [17, 27]. DFA was previously shown to produce reliable estimates of scaling behavior in little penguin and Adélie penguin dive sequences [30, 37]. Since including the smallest and largest scales in the estimation of fractal scaling exponents can introduce mathematical biases [40], we first calculated best-scaling regions for each treatment group using methods provided in [44] and used those rather than the full set of measurement scales available to estimate α_{DFA}. DFA was run using the package 'fractal' [45] in R statistical software v.3.1.1 [46]. Details of the analytical approach used here, including DFA calculation, the subsequent validation of scaling, and its relationship to other fractal dimension estimates are provided in [37] and the associated Supplementary Materials. Example dataset will be provided upon request to anyone wishing to reproduce our method.

All statistical analyses were conducted in R 3.1.1. We constructed General Linear Mixed effects models (GLMM) using the package 'nlme' [47] to investigate

whether variation in α_{DFA} existed between groups in each experiment. In all models, we set individual identity and trip date as crossed random factors to account for pseudoreplication and temporal variation, respectively, and trip duration as a covariate to control for the effects of sequence length on scaling exponents [37]. In the logger size and/or position experiments, we included the following factors in the models: logger size (for both species), logger position and sex of the individual (for little penguins only). For the flipper band experiments, we added banded state (banded or not) as a fixed factor and trip duration as covariate. We also tested for interactions between logger size/position and sex via likelihood ratio tests using the package 'lmtest' [48] after first running the GLMM with and without these interaction terms. Values of α_{DFA} are presented as mean ± SE, and we set the alpha level for all statistical analyses at 0.05.

Results

Fractal analyses showed values of α_{DFA} ranging between 0.74 and 0.94 (mean = 0.86, SE = 0.008) for little penguins during the logger experiment and values of α_{DFA} ranging between 0.74 and 0.97 (mean = 0.88, SE = 0.008) for little penguins during the flipper band experiment. Adélie penguins exhibited higher mean values of α_{DFA} ranging between 0.91 and 0.98 (mean = 0.94, SE = 0.005). These values indicate that dive sequences are long-range dependent and resemble persistent fractional Gaussian noise, as shown previously [30, 37]. The likelihood ratio test showed no difference between statistical models with and without interaction terms ($p = 0.16$), so we present results from the more parsimonious models without the interaction terms in which the main effects can be better interpreted.

We observed a significant difference between dive sequences produced by little penguins carrying loggers of different sizes (Table 1; GLMM: α_{DFA}, $df = 21$, $t = 2.22$, $p = 0.04$; mean α_{DFA} large logger = 0.85 ± 0.008; mean α_{DFA} small logger = 0.94 ± 0.008): little penguins carrying larger loggers exhibited lower values of α_{DFA}, reflecting greater stochasticity in dive sequences than those carrying smaller loggers. Figure 1 illustrates this difference as well as the process of DFA using representative little penguins equipped with a small and large logger, respectively. Logger position, on the other hand, was not significantly associated with complexity in dive sequences, although little penguins carrying loggers in middle positions showed a tendency toward lower α_{DFA} values compared with those carrying loggers in lower positions (Table 1; GLMM: α_{DFA}, $df = 21$, $t = 1.79$, $p = 0.09$; mean α_{DFA} middle position = 0.85 ± 0.015; mean α_{DFA} low position = 0.87 ± 0.008). In addition, our statistical model showed that males displayed higher values of α_{DFA} than females (Table 1; GLMM: α_{DFA}, $df = 21$, $t = -4.87$, $p = 0.0001$; mean α_{DFA} male = 0.89 ± 0.007; mean α_{DFA} female = 0.84 ± 0.009), whereas trip duration had no effect (Table 1; GLMM: α_{DFA}, $df = 21$, $t = -0.05$, $p = 0.96$).

We did not observe any effects of flipper banding on α_{DFA} values in either the short-term (Table 1; GLMM: α_{DFA}, $df = 11$, $t = -0.91$, $p = 0.38$; mean α_{DFA} non-banded = 0.88 ± 0.021; mean α_{DFA} banded = 0.86 ± 0.013) or long-term (Table 1; GLMM: α_{DFA}, $df = 3$, $t = 0.44$, $p = 0.69$; mean α_{DFA}

Table 1 Summary of GLMM statistics for all experiments

Experiment	Variable	Est	SE	*df*	*t* value	*p* value
Little penguin logger size	Intercept	0.8733	0.1973	21	4.42	*0.0002*
	Size (large vs small)	0.0285	0.0128	21	2.22	*0.04*
	Position (middle vs low)	0.0232	0.013	21	1.79	0.09
	Trip duration	−0.0006	0.0132	21	−0.05	0.96
	Sex (male vs female)	−0.0623	0.0128	21	−4.87	*0.0001*
Adélie penguin logger size	Intercept	0.9628	0.0129	7	74.58	*0*
	Size (large vs small)	0.0053	0.0084	7	0.64	0.54
	Trip duration	−0.0008	0.0003	7	−2.46	*0.04*
Little penguin flipper band short-term	Intercept	1.0824	0.344	11	3.15	*0.01*
	State (non-banded vs banded)	−0.024	0.0265	11	−0.91	0.38
	Trip duration	−0.013	0.0226	11	−0.57	0.58
Little penguin flipper band long-term	Intercept	0.7463	0.3493	14	2.14	0.05
	State (non-banded vs banded)	0.011	0.025	3	0.44	0.69
	Trip duration	0.0076	0.0234	3	0.33	0.76

Italicized text highlights significant p values.

Est estimate, *SE* Standard error, *df* degree of freedom.

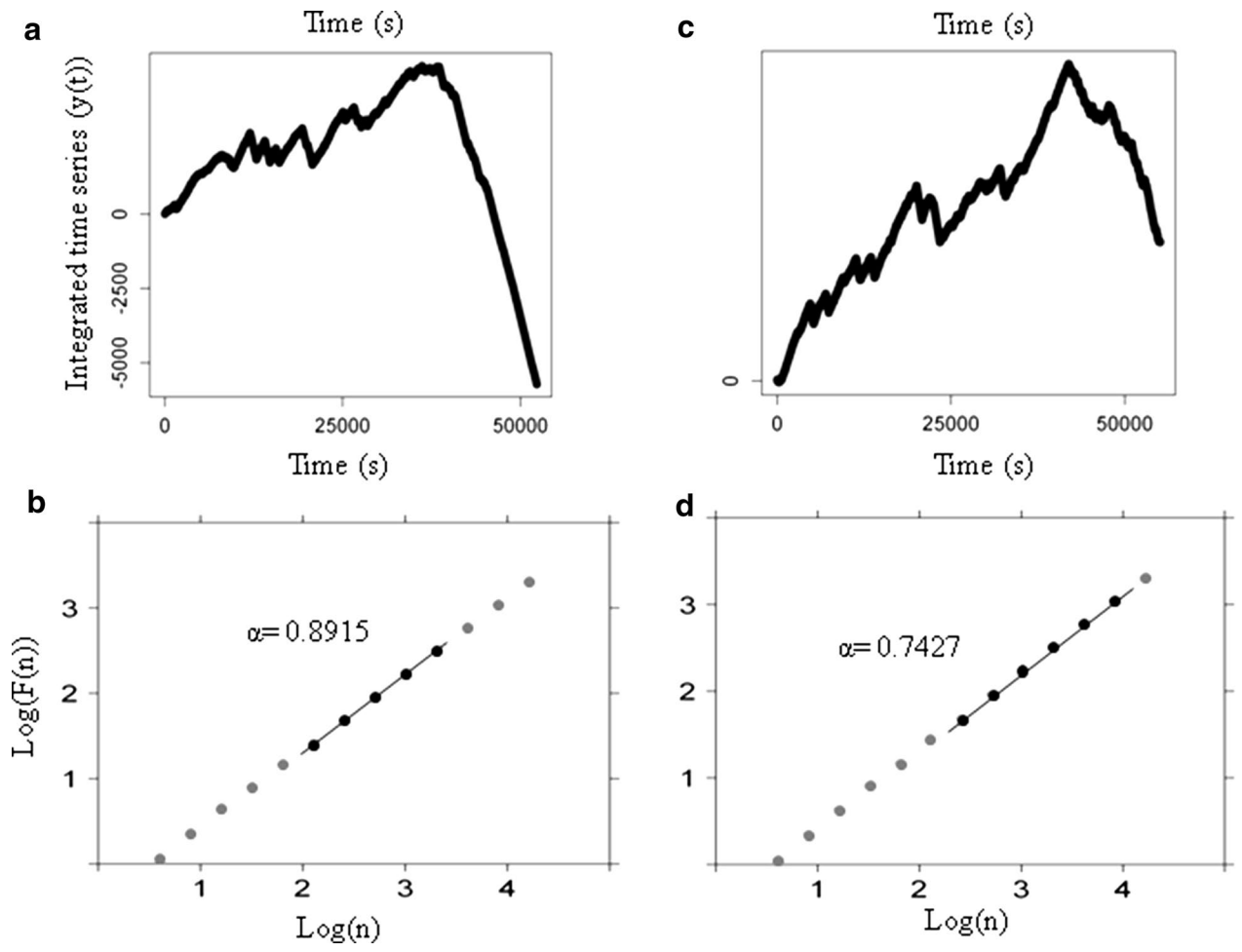

Fig. 1 Detrended fluctuation analysis (DFA) of foraging sequences from a little penguin carrying a small logger (*first column*) and a little penguin carrying a large logger (*second column*). **a**, **c** Integrated dive sequences ($y(t)$) generated by the accumulation of a binary time series of diving (+1) vs surface time (−1) across the entire length of the single-day foraging trips performed by each little penguin. **b**, **d** Log–log plots of the average fluctuation $F(n)$ at each scale (window size) across the dive sequences on the *y* axes as a function of scale (n) on the *x* axes. The values of α_{DFA} reflect the slope of the regression lines, with lower α_{DFA} reflecting greater complexity (stochasticity). Note that only the points in *black* were used to fit the regression line to avoid biases introduced at small and large scales; these 'best scaling regions' were calculated using methods described in the text.

non-banded = 0.86 ± 0.018; mean α_{DFA} banded = 0.88 ± 0.014) experiments. Our covariate, trip duration, was also not associated with values of α_{DFA} in either experiment, respectively (Table 1; GLMM: α_{DFA}, $df = 11$, $t = -057$, $p = 0.58$; GLMM: α_{DFA}, $df = 3$, $t = 0.33$, $p = 0.76$).

Finally, logger size had no effect on the α_{DFA} values estimated for Adélie penguin diving sequences (Table 1; GLMM: α_{DFA}, $df = 7$, $t = 0.64$, $p = 0.54$; mean α_{DFA} large logger = 0.938 ± 0.008; mean α_{DFA} small = 0.937 ± 0.008), but longer trip durations were negatively associated with α_{DFA} values (Table 1; GLMM: α_{DFA}, $df = 7$, $t = -2.46$, $p = 0.04$), i.e., the longer the trip the greater the stochasticity of the dive sequence.

Discussion

We demonstrate here that the size of back-mounted recording devices is associated with variation in the temporal organization of foraging behavior in little penguins. Unlike most previous studies of fractal time in animal behavior, which demonstrated alterations toward more stereotypical sequential patterns in the presence of various stressors (i.e., complexity loss), we show here that dive sequences were more complex, exhibiting greater stochasticity, in birds with larger loggers. The hydrodynamic handicaps imposed by large loggers, and by extrapolation perhaps loggers in general though studies of this nature necessarily lack true controls (i.e., birds without loggers), thus seem to add an extra element of noise into

the diving sequences of little penguins. However, the lack of effects of logger position in little penguins, logger size in Adélie penguins and, surprisingly, flipper bands in little penguins suggests that animal-attached devices do not universally induce such organizational changes in seabird foraging behavior, despite having clear effects on other dive parameters and potentially, for flipper bands at least, fitness outcomes [49–51].

The use of back-mounted recording devices on penguins and other marine animals increases drag, which should increase swimming energy expenditure at a given velocity [35, 52]. With increasing energy expenditures, air-breathing marine predators such as penguins may need to reduce dive durations as oxygen stores are depleted more rapidly than when they are not handicapped, and/or increase post-dive duration periods at the surface to replenish oxygen stores in provision of future dives. This may in part explain our results for little penguins; because of the increased foraging effort observed in little penguins with large loggers, evidenced by the greater numbers of dives per foraging trip, hourly dive rates, total time spent underwater and at least in males longer foraging trips [32, see also 53], the between-dive durations were less variable (the mean standard deviations for individuals equipped with large loggers vs small loggers were 72.88 ± 10.11 vs 105.13 ± 9.08 s, respectively), leading to more randomized sequences of behavior. All else being equal, surface durations are much freer to vary (diverge from a random distribution) than are dive durations due to the physiological constraints of diving activity (i.e., oxygen depletion, CO_2 and lactic acid accumulation [54]). Given the small differences in body size between sexes [55], the sex differences observed here could be explained by variation in dietary preference, e.g., males having a different diet than females or perhaps feeding on same species but larger prey. Unfortunately, we do not have any dietary information for the birds we monitored, though dietary differences between sexes have been shown to be minimal in little penguins [56].

Alternatively, rather than reducing dive durations and other frequency-based dive parameters, Adélie penguins equipped with large loggers are known to compensate for this handicap by reducing swim speeds, thereby maintaining similar per dive energy expenditures as birds equipped with small loggers [33]. Both strategies would reduce achievable dive depths and time spent with prey, thus limiting foraging efficiency [32, 33], but such limitations would likely be far less detrimental to Adélie penguins, which feed on densely packed, slow-moving prey (krill [57, 58]). This effect should be stronger on little penguins that indeed showed organizational changes in their dives as they feed on fast-moving prey (fish [55]). At a given position, the drag caused by back-mounted devices, and resultant effects on dive profiles, should depend primarily on the ratio of logger to body size. In the present study, large loggers accounted for a significantly larger cross-section of the frontal area of little penguins (4.9%) than the much larger Adélie penguins (only 1.4%). Small body size already disadvantages diving seabirds, so little penguins may not have the option to decrease swim speeds to compensate for the extra drag as Adélie penguins seem to do [33], and must instead make organizational changes to their dive profiles. Interestingly, we detected an effect of trip duration on the sequential organization of foraging behavior in Adélie penguins and the direction of the effect may seem counterintuitive when comparing with the results of [37]. However, MacIntosh et al. [37] conducted their analysis on little penguins during the guard stage where birds are restricted to a 1-day trip. It is possible that variation in trip duration and the associated variation in foraging effort in Adélie penguins [59] may have cause this statistical effect to appear. Future studies should investigate this as variable trip lengths could potentially influence the conclusions driven from the use of the DFA method. For the present analysis, we note that the effect should be limited as the estimate value only changes by 0.0008.

Despite that logger position was not significantly associated with foraging sequence complexity in little penguins, we hesitate to reject this possibility outright for two reasons: (1) that the results showed a statistical trend and (2) that the difference exhibited consistency with the effect of logger size in that the sign of the difference was the same, i.e., toward greater stochasticity in the middle position, which we predicted would impose a greater hydrodynamic handicap than loggers placed lower on the back. Still, that the effect of logger position was weaker than that of logger size also mirrors the original study, in which the former had little impact on the dive parameters examined [32]. However, penguins with small loggers positioned middle on their backs did dive to significantly greater depths than those with large loggers on the same position and displayed a tendency toward increased dive durations as well, while no difference was observed when the loggers were positioned lower [32]. As discussed above, resultant changes in the sequential distributions of dive and between-dive times may account for the tendency toward greater stochasticity observed here in penguins equipped with loggers in the middle of their backs as well, however marginal these differences may be. Since the change in drag is expected to be less dramatic for the two logger positions than the two logger sizes [32], the weaker influence of position on dive sequence complexity is not surprising.

What is perhaps most surprising in our study is the lack of effect of flipper bands on observed dive sequences.

Using the same dataset, Fallow et al. [36] highlighted the immediate effects of flipper banding on the diving behavior of little penguins using conventional measures; notably, dive durations increased significantly while dive efficiency, defined as bottom phase duration/(dive duration + post-dive duration), decreased significantly in newly banded birds. Apparently, these differences are not necessarily associated with organizational changes in dive sequences. One major difference between the previously observed flipper band and large logger effects is that increased logger size induced significant increases in overall diving effort, defined as the cumulative time spent underwater during the trip, and total numbers of dives performed, neither of which differed in the flipper band experiment [32, 36]. Indeed, dive durations and between-dive durations increased in the flipper band experiment, meaning that the sequential distribution and variance of both dive and surface durations may not have changed, leaving the global structure of the foraging trip unchanged as well. This also suggests that global structural changes in the organizational complexity of dive sequences need not be associated with other changes in foraging behavior, e.g., those induced by flipper bands, that are known to significantly affect survival and reproduction (e.g., [49–51]).

While variation in performance outcomes (e.g., body mass gain) was not measured in the original study [32], the alterations in the organizational structure of foraging sequences we observed in little penguins equipped with large loggers, and potentially those placed in positions that further increase drag, can theoretically affect the overall performance of birds in their ability to detect and capture prey. Emergent fractal patterns in the movement behavior of numerous animal species are thought to reflect an underlying strategy aimed at maximizing prey encounters, particularly with heterogeneous prey fields [5, 8–11]. Observed complexity signatures under normal conditions are thus predicted to reflect theoretical optimal behavior patterns [14, 25], while deviations from such theoretical optimal patterns have been associated on numerous occasions with pathological or otherwise challenging intrinsic conditions, such as intense parasitic infection [6, 25], increased physiological stress [30], anthropogenic disturbance [29] and even advanced reproductive state [6, 25]. While increased complexity might approximate an optimal solution to some imposed stressors, e.g., the increased vigilance sequences observed in hens moved to novel enclosures [26], these tendencies toward stochasticity also appear to be associated with decreased energetic efficiency. Thus, hens in novel environments also significantly increased their total vigilance behavior, which would interfere with normal feeding patterns [26]. Here, little penguins carrying large loggers were probably forced to compensate with more frequent dives and longer foraging trips, presumably to achieve baseline energy gains. These compensatory behavior patterns are unlikely to be optimal in the long term.

Conclusions

Hydrodynamic handicaps caused by carrying externally attached devices exhibited variable influence on the organizational properties of penguin foraging sequences. Relative drag caused by back-mounted devices is likely an important component of dive sequence complexity for smaller species, decreasing variability in the alternation between diving and surface intervals and thus creating greater stochasticity in patterns of foraging behavior. It is also important to remember that there was no true control in this experiment, since all birds were equipped with loggers of variable sizes and positions. Given our results, it seems likely at least for little penguins that unequipped birds might exhibit a different set of fractal properties altogether, with even less noise in their dive sequences. This might even have confounded our flipper band experiment, for which there was a true control, if the effects of loggers interacted in some way with or overshadowed the effects of flipper bands, but this cannot be tested. Ultimately, we show here that increased noise in dive sequences, as opposed to the more commonly observed increased stereotypy [6, 25, 29, 30], is a potential outcome of coping with an added stressor. Further application of fractal tools to temporal sequences of behavior is needed to examine how animals cope with various realizations of environmental change, particularly organisms used as indicator species for environmental change.

Authors' contributions

YRC, AK and AC conceived the experiment, collected the data and analyzed the frequency-based measures presented. YRC and AK arranged the dataset for fractal analysis. XM and AM conducted all fractal analyses and wrote the manuscript. All authors contributed to manuscript discussion and revision. All authors read and approved the final manuscript.

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Competing interests
The authors declare that they have no competing interests.

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References

1. Mandelbrot BB (1977) The fractal geometry of nature. W.H. Freeman and Company, New York
2. Viswanathan GM, Afanasyev V, Buldyrev SV, Murphy EJ, Prince P, Stanley HE (1996) Lévy flight search patterns of wandering albatrosses. Nature 381:413–415
3. Boyer D, Miramontes O, Ramos-Fernández G, Mateos JL, Cocho G (2004) Modeling the searching behaviour of social monkeys. Phys A Stat Mech Appl 342(1–2):329–335
4. Bartumeus F, Levin SA (2008) Fractal reorientation clocks: linking animal behaviour to statistical patterns of search. Proc Natl Acad Sci USA 105(49):19072–19077
5. Sims DW, Southall EJ, Humphries NE, Hays GC, Bradshaw CJA, Pitchford JW et al (2008) Scaling laws of marine predator search behaviour. Nature 451(7182):1098–1103
6. MacIntosh AJJ, Alados CL, Huffman MA (2011) Fractal analysis of behaviour in a wild primate: behavioural complexity in health and disease. J R Soc Interface 8(63):1497–1509
7. Wearmouth VJ, McHugh MJ, Humphries NE, Naegelen A, Ahmed MZ, Southall EJ et al (2014) Scaling laws of ambush predator 'waiting' behaviour are tuned to a common ecology. Proc R Soc B 281(1782):20132997
8. Bartumeus F (2007) Lévy processes in animal movement: an evolutionary hypothesis. Fractals 15(2):151–162
9. Viswanathan GM, Raposo EP, Da Luz MGE (2008) Lévy flights and superdiffusion in the context of biological encounters and random searches. Phys Life Rev 5(3):133–150
10. Viswanathan GM, Da Luz MGE, Raposo EP, Stanley HE (2011) The physics of foraging. Cambridge University Press, Cambridge
11. Humphries NE, Weimerskirch H, Queiroz N, Southall EJ, Sims DW (2012) Foraging success of biological Lévy flights recorded in situ. Proc Natl Acad Sci USA 109(19):7169–7174
12. Dicke M, Burrough PA (1988) Using fractal dimensions for characterizing tortuosity of animal trails. Physiol Entomol 13:393–398
13. Crist TO, Guertin DS, Wiens JA, Milne BT (1992) Animal movement in heterogeneous landscapes: an experiment with *Eleodes* beetles in shortgrass prairie. Funct Ecol 6:536–544
14. Johnson AR, Wiens JA, Milne BT, Crist TO (1992) Animal movements and population dynamics in heterogeneous landscapes. Landsc Ecol 7:63–75
15. Wiens JA, Crist TO, Milne BT (1993) On quantifying insect movements. Environ Entomol 22(4):709–715
16. Wiens JA, Crist TO, With KA, Milne BT (1995) Fractal pattern of insect movement in microlandscape mosaics. Ecology 76:663–666
17. Asher L, Collins LM, Ortiz-Pelaez A, Drewe JA, Nicol CJ, Pfeiffer DU (2009) Recent advances in the analysis of behavioural organization and interpretation as indicators of animal welfare. Interface 6(41):1103–1119
18. MacIntosh AJJ (2014) The fractal primate: interdisciplinary science and the math behind the monkey. Primate Res 1–26
19. Camazine S, Deneubourg J-L, Franks NR, Sneyd J, Theraulaz G, Bonabeau E (2001) Self-organization in biological systems. Princeton University Press, Princeton
20. Bradbury JW, Vehrencamp SL (2014) Complexity and behavioural ecology. Behav Ecol 00:1–8
21. West BJ (1990) Physiology in fractal dimensions: error tolerance. Ann Biomed Eng 18:135–149
22. Peng CK, Havlin S (1995) Quantification of scaling exponents and crossover phenomena in nonstationary heartbeat time series. Chaos 5:82–87
23. Hausdorff JM, Peng CK, Ladin Z, Wei JY, Goldberger AL (1995) Is walking a random walk? Evidence for long-range correlations in stride interval of human gait. J Appl Physiol 79:349–358
24. Abásolo D, Hornero R, Escudero J, Espino P (2008) A study on the possible usefulness of detrended fluctuation analysis of the electroencephalogram background activity in Alzheimer's disease. IEEE Trans Biomed Eng 55(9):2171–2179
25. Alados CL, Escos JM, Emlen JM (1996) Fractal structure of sequential behaviour patterns: an indicator of stress. Anim Behav 51(2):437–443
26. Rutherford KMD, Haskell MJ, Glasbey C, Jones RB, Lawrence AB (2003) Detrented fluctuation analysis of behavioural responses to mild acute stressors in domestic hens. Appl Anim Behav Sci 83(12):125–132
27. Rutherford K, Haskell M, Glasbey C, Jones RB, Lawrence AB (2004) Fractal analysis of animal behaviour as an indicator of animal welfare. Anim Welf 13:99–103
28. Rutherford KMD, Haskell MJ, Glasbey C, Lawrence AB (2006) The responses of growing pigs to a chronic-intermittent stress treatment. Physiol Behav 89(5):670–680
29. Seuront L, Cribb N (2011) Fractal analysis reveals pernicious stress levels related to boat presence and type in the Indo-Pacific bottlenose dolphin, *Tursiops aduncus*. Physica A 390(12):2333–2339
30. Cottin M, MacIntosh A, Kato A, Takahashi A, Debin M, Raclot T, Ropert-Coudert Y (2013) Corticosterone administration leads to a transient alteration of foraging behaviour and complexity in a diving seabird. Mar Ecol Prog Ser 496:249–262
31. Kembro JM, Perillo MA, Pury PA, Satterlee DG, Marín RH (2009) Fractal analysis of the ambulation pattern of Japanese quail. Br Poult Sci 50(2):161–170
32. Ropert-Coudert Y, Knott N, Chiaradia A, Kato A (2007) How do different data logger sizes and attachment positions affect the diving behaviour of little penguins? Deep Sea Res Part II Topical Stud Oceanogr 54(3–4):415–423
33. Ropert-Coudert Y, Wilson RP, Yoda K, Kato A (2007) Assessing performance constraints in penguins with externally-attached devices. Mar Ecol Prog Ser 333:281–289
34. Culik BM, Wilson RP (1991) Swimming energetic and performance of instrumented Adélie penguins (*Pygoscelis adeliae*). J Exp Biol 158:355–368
35. Bannasch R, Wilson RP, Culik B (1994) Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. J Exp Biol 194(1):83–96
36. Fallow PM, Chiaradia A, Ropert-Coudert Y, Kato A, Reina RD (2009) Flipper bands modify the short-term diving behaviour of little penguins. J Wildl Manag 73(8):1348–1354
37. MacIntosh AJJ, Pelletier L, Chiaradia A, Kato A, Ropert-Coudert Y (1884) Temporal fractals in seabird foraging behaviour: diving through the scales of time. Nat Sci Rep 2013(3):38
38. Peng CK, Buldyrev SV, Goldberger AL, Havlin S, Sciortino F, Simons M et al (1992) Long-range correlations in nucleotide sequences. Nature 356:168–170
39. Taqqu M, Teverovsky V, Willinger W (1995) Estimators for long-range dependence: an empirical study. Fractals 3(4):785–788
40. Cannon MJ, Percival DB, Caccia DC, Raymond GM, Bassingthwaighte JB (1997) Evaluating scaled windowed variance methods for estimating the Hurst coefficient of time series. Phys A 241(3–4):606–626
41. Eke A, Hermán P, Bassingthwaighte JB, Raymond GM, Percival DB, Cannon M et al (2000) Physiological time series: distinguishing fractal noises from motions. Pflügers Arch Eur J Physiol 439:403–415
42. Delignières D, Torre K, Lemoine L (2005) Methodological issues in the application of monofractal analyses in psychological and behavioral research. Nonlinear Dyn Psychol Life Sci 9(4):451–477
43. Kiraly A, Janosi IM (2004) Detrended fluctuation analysis of daily temperature records: geographic dependence over Australia. Meteorol Atmos Phys 88(3–4):119–128
44. Seuront L (2010) Fractals and multifractals in ecology and aquatic science. CRC Press, Boca Raton
45. Constantine W, Percival D (2014) Fractal Time Series Modeling and Analysis version 2.0-0.http://CRAN.R-project.org/package=fractal. Accessed 10 Oct 2014
46. R Development Core Team (2014) R: A Language and Environment for Statistical Computing. Vienna: the R Foundation for Statistical Computing. http://www.R-project.org/. Accessed 5 Mar 2015
47. Pinheiro J, Bates D, DebRoy S, Sarkar D, EISPACK authors R-Core: nlme (2015) Linear and Nonlinear Mixed Effects Models version 3.1-118. http://cran.r-project.org/web/packages/nlme/index.html. Accessed 5 Mar 2015

48. Hothorn T, Zeilis A, Farebrother RW, Cummins C, Millo G, Mitchell D (2015) Testing linear regression models version 0.9-33. http://cran.r-project.org/web/packages/lmtest/lmtest.pdf. Accessed 5 Mar 2015
49. Saraux C, Le Bohec C, Durant JM, Viblanc VA, Gauthier-Clerc M, Beaune D et al (2011) Reliability of flipper-banded penguins as indicators of climate change. Nature 469:203–206
50. Gauthier-Clerc M, Gendner J-P, Ribic CA, Fraser WR, Woehler EJ, Descamps S et al (2004) Long-term effects of flipper bands on penguins. Proc R Soc Biol Sci 271(Suppl):423–426
51. Dann P, Sidhu LA, Jessop R, Renwick L, Healy M, Dettmann B et al (2014) Effects of flipper bands and injected transponders on the survival of adult Little Penguins *Eudyptula minor*. Ibis 156(1):73–83
52. Wilson RP, Grant WS, Duffy DC (1986) Recording devices on free-ranging marine animals: dies measurements affect foraging performance. Ecology 67:1091–1093
53. Kato A, Watanuki Y, Nishumi I, Kuroki M, Shaughnessy P, Naito Y (2000) Variation in foraging and parental behavior of king cormorants. Auk 117:718–730
54. Kooyman GL (1989) Diverse divers. Springer-Verlag, Berlin
55. Arnould JPY, Dann P, Cullen JM (2004) Determining the sex of little penguin (*Eudyptula minor*) in northern Bass Strait using morphometric measurements. Emu 104:261–265
56. Chiaradia A, Forero MG, Hobson K, Swearer SE, Hume F, Renwick L et al (2012) Diet segregation between two colonies of little penguins *Eudyptula minor* in southeast Australia. Austral Ecol 37(5):610–619
57. Cherel Y (2008) Isotopic niches of emperor and Adélie penguins in Adélie Land, Antarctica. Marine Biol 154(5):813–821
58. Wilson RP, Ropert-Coudert Y, Kato A (2002) Rush and grab strategies in foraging marine endotherms: the case for haste in penguins? Anim Behav 63:85–95
59. Ropert-Coudert Y, Wilson RP, Daunt F, Kato A (2004) Patterns of energy acquisition by penguins: benefits of alternating short and long foraging trips. Behav Ecol 15:824–830

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