Leg rings impact the diving performance of a foot-propelled diver

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Leg rings are frequently used to mark aquatic birds in order to identify individuals, and study population dynamics and migration patterns, with the proviso being that the rings should not affect the birds. The effects of tags and rings are of particular interest in diving birds because any change in body shape could impact swimming efficiency and costs, as water is almost a thousand times denser than air. We attached tri-axial accelerometers to both ringed and unringed breeding Imperial Shags *Leucocarbo atriceps* to assess dive performance based on descent angle, descent rate, power stroke rate, power stroke peak acceleration amplitude and Vectorial Dynamic Body Acceleration (VeDBA) as a proxy for energy expenditure. Ringed birds, especially females, had a higher foot-stroke amplitude than unringed animals. In addition, the overall efficiency of the ringed individuals, as expressed by the descent rate per unit VeDBA, was compromised (by 3.5% in females and 4.3% in males) compared with unringed birds. We conclude that leg rings change the diving performance of Imperial Shags, although the effect is small and may not affect reproductive success. However, given that birds are typically ringed for life, we urge researchers to be particularly careful about the potential cumulative effect of attaching leg rings to foot-propelled diving species.

Keywords: diving behaviour, energy expenditure, leg rings, *Leucocarbo atriceps*, Imperial Shag, VeDBA.

Tagging aquatic birds with flipper bands or leg rings allows scientists to study *inter alia* migration patterns, estimate survival rates and obtain information about the social structure of a population (Patterson 1978, McClure 1984). However, several studies have demonstrated that flipper bands

on wing-propelled marine birds, such as penguins, increase the costs of underwater locomotion (for a review see Jackson & Wilson 2002). This has been primarily attributed to the band structure disturbing the water flow around the wing and body during swimming, increasing power use and negatively affecting manoeuvring capacities during prey capture (Culik *et al.* 1993), ultimately affecting penguin breeding success and survival (Saraux *et al.* 2011). In addition, flipper bands have been

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associated with physical damage to the wing, mainly during moult, due to restrictions in blood circulation (Ainley et al. 1983).

Diving costs are generally considered to be higher in foot-propelled diving birds than for wing-propelled species (Lovvorn & Liggins 2002) because the thrust produced by wings is much greater than the thrust produced by the feet (Weihs & Webb 1983). This suggests that foot-propelled divers might be more susceptible to any detrimental effects of rings compared with wing-propelled birds. However, in contrast to the numerous studies analysing the effect of flipper bands on the diving behaviour of penguins (Culik et al. 1993, Fallow et al. 2009), only one previous study has examined the effect of a small leg-attached device on the diving behaviour of the Great Cormorant *Phalacrocorax carbo carbo* (Ropert-Coudert et al. 2009). In that study, the authors found no significant effect of a tag attached to a leg ring on the diving behaviour (e.g. dive depth, duration and efficiency) of a small sample of birds ($n = 6$ with and without tags, respectively). However, this work did not focus on analysing fine-scale underwater movement parameters such as dynamic body acceleration (which gives an integrated measure of the dynamism of body motion in all three spatial dimensions) as a proxy for energy expenditure (Wilson et al. 2006, 2020) or stride frequency (i.e. number of foot-strokes per second) (Cook et al. 2010).

The Imperial Shag *Leucocarbo atriceps* is a foot-propelled diver that belongs to the blue-eyed cormorant group, which includes 13 taxa (Orta 1992), all of which are spectacular divers, with records of some reaching depths of more than 140 m (Tremblay et al. 2005) and remaining underwater for up to 6 min (Wanless et al. 1992). Such performance might make these species particularly susceptible to the detrimental effects of rings and seems especially germane given that rings are commonly used in this taxon for behavioural ecology studies (Svagelj & Quintana 2011, Harris et al. 2014) and as a base on which to deploy tags for post-breeding migration studies (Daunt et al. 2005, Harris et al. 2013).

The aim of the present study was to determine whether banding a foot-propelled diver, the Imperial Shag, with a ring on both tarsi influences diving performance, particularly with respect to energy expenditure. For this, we first examined whether general diving parameters such as the total number of dives performed during a foraging trip, the duration of each diving phase and the rate of change of depth differed between ringed and unringed birds. Secondly, we studied a number of intra-dive measures of performance using: (i) a proxy for energy expenditure (VeDBA, Vectorial Dynamic Body Acceleration; Qasem et al. (2012)), (ii) foot stroke parameters (period and amplitude), (iii) bird pitch angle and (iv) the vertical descent rate in the water column (because descents require high power as birds work against substantial upthrust to gain depth most efficiently; Wilson et al. 2006, Cook et al. 2008, Gómez-Laich et al. 2013). We hypothesized that the presence of a ring on both tarsi affects the general dive parameters of Imperial Shags. Therefore, we predicted that the number of dives per foraging trip, the duration of each dive phase, the maximum depth reached during each dive and the rate of change of depth differ between ringed and unringed birds. Additionally, we hypothesized that the presence of a ring on both tarsi affects the relationship between (our proxy for) energy expenditure and depth during the descent phase of dives. Consequently, we predicted that while descending in the water column, ringed birds expend more energy than unringed birds. We also predicted that the presence of a ring on both tarsi affects the descent phase foot stroke parameters such as frequency (foot strokes per unit time) and amplitude (stroke strength), and has an effect on the pitch angle and on the rate of change of depth.

METHODS

Fieldwork was conducted at the Punta León Imperial Shag colony (43°04′S, 64°02′W), Chubut, Argentina, during November 2017. To conduct various behavioural ecology studies (Svagelj & Quintana 2011, Harris et al. 2014), over the last 15 years, several breeding birds from this colony were captured (selected randomly) and ringed with a metal ring (aluminium, 16 mm high × 21 mm diameter, 4.0 g) on the left leg tarsus and a plastic ring (Darvic, 29 mm high × 21 mm diameter, 3.7 g) on the right leg tarsus. Capitalizing on this, 20 ringed birds (10 females and 10 males) and 20 unringed birds (10 females and 10 males) were equipped with AXY-TREK 3D tags (40 mm long × 20 mm wide × 8 mm tall, 25 g, TechnoSmart, Rome, Italy) during the first 10 days of the chick-rearing

period. The total weight of the device was less than 1.4% and 1.1% of the average adult female and male body mass, respectively (Svagelj & Quintana 2007), both percentages being markedly less than the generally accepted recommendation of 3% (Kenward 2001). Unfortunately, we did not document either the length of foraging trips or the body mass change of a control group of unequipped birds, so the effects of the devices in this regard could not be evaluated. Devices were programmed to record tri-axial acceleration (at 25 Hz) as well as position (latitude, longitude), pressure and temperature (at 1 Hz). The sex of each animal was determined by the vocalizations (males 'honk' and females 'hiss') (Malacalza & Hall 1988, Svagelj & Quintana 2007). Each Shag was slowly removed from its nest using a specially designed crook, consisting of a hook at the end of a 2-m pole. The hook was placed gently around the bird's neck and used to bring the animal closer to the handler. Once close enough to be handled, the Shag's neck was taken out of the hook by grasping the neck behind the head with one hand and using the second hand to gather the wings up against the body. Loggers were attached to the feathers of the lower back with adhesive Tesa 4651 tape following Wilson *et al.* (1997). The attachment procedure took around 5 min per bird. The total handling time was always less than 10 min per animal and all birds were tagged within a 5-day period. After tag attachment, birds were left to forage for a single foraging trip before the devices were retrieved and each bird was weighed using a spring scale. Imperial Shags from this colony show a high degree of consistency in the areas they visit during the breeding season, particularly during the early chick-rearing period (Harris *et al.* 2014). As Imperial Shags from Punta León almost exclusively perform benthic dives (Shepard *et al.* 2010, Gómez-Laich *et al.* 2015), the fact that they return to the same areas means that they are diving to the same depths. Taking this into account, all the analysed diving parameters (see below) of one foraging trip from each bird were considered to be representative of an average foraging trip diving behaviour. We note that this assumption has some limitations. For example, birds could return to the same area and exploit the same depths but perform a different number of dives or even descend to the same depth in a slightly different way. Additionally, although we cannot rule out that the first foraging

trip post-tagging might have been affected by the stress associated with capture and handling, any potential effect of handling would have been consistent across ringed and unringed individuals. All birds carrying devices returned to the colony and resumed normal nest attendance.

Data processing

Unless stated otherwise, all data processing and statistical analyses were conducted in R 3.6.1 (R Core Team 2019). The time spent in the different phases of a dive (descent, bottom and ascent), the maximum depth reached during a dive, and the rate of change of depth for the descent phase were calculated using the program MTDIVE (Jensen Software Systems). Female Imperial Shags rarely dive below 30 m depth and males rarely reach depths in excess of 45 m (Quintana *et al.* 2011, Gómez Laich *et al.* 2012). Taking this into account, only female and male dives where the maximum depth was less than 30 and 45 m, respectively, were considered for all analyses of the descent diving phase. As pressure data were recorded at 1 Hz and acceleration data at 25 Hz, for each descent dive phase, missing pressure data were linearly interpolated using the *na.approx* function from the *zoo* library (Zeileis & Grothendieck 2005). This interpolation allowed us to compute what we defined as instantaneous depth.

VeDBA (Qasem *et al.* 2012) quantifies the animal-induced dynamic component of the acceleration of a tag-wearing animal, this being linearly related to the energy expenditure of the animal (see Wilson *et al.* 2020, and references therein). To calculate VeDBA, we isolated the dynamic acceleration component from the static component for all dive descent phases as described by Shepard *et al.* (2008). VeDBA was then calculated following methods described by Qasem *et al.* (2012) and smoothed over 1 s to eliminate individual strides and thereby better estimate the costs of movement (Wilson *et al.* 2020).

When cormorants descend the water column, the body is accelerated downward and forward during the power stroke of the feet and decelerated during the glide or recovery phase (Watanuki *et al.* 2005). As such, each foot stroke can be recognized either by a negative peak in the heave acceleration channel or a positive peak in the surge acceleration channel. In this work, we used the raw heave acceleration channel to calculate the

number and amplitude of peaks per second during the descent phase of each dive using the *Gundog.Peaks* function (Gunner et al. in press). As stroking activity is most intense nearer the surface during the descent phase (Cook *et al.* 2010), and recording data at 25 Hz is not appropriate to detect high-frequency strokes, peak number and amplitude were calculated only when birds were deeper than 5 m.

The pitch angle during the descent phase of each dive was computed using the static acceleration component of each channel following the equation presented in Gunner *et al.* (2020) and smoothed over 1 s – only one value per second was used in the statistical models. Finally, the vertical transit rate (m/s) during the descent phase was calculated by calculating the rate of change of depth every second.

Statistical analysis

Previous studies found intersexual differences in the diving behaviour of Imperial Shags (Quintana *et al.* 2011, Gómez-Laich *et al.* 2012, 2013) so we analysed each sex separately. We decided to run separate models for each sex instead of adding sex as a covariate due to the substantially different number of dives performed by each sex to different depths and due to the fact that dives deeper than 30 m depth were only performed by the males.

To study the differences between ringed and unringed birds in general diving parameters, such as the total number of dives performed per foraging trip, the duration of each diving phase and the rate of change of depth, all recorded dives were included. Differences between the total number of dives undertaken between ringed and unringed birds were tested using Mann–Whitney tests. Differences in the different diving phase durations (descent, bottom and ascent), maximum dive depth and mean rate of change of depth, were tested by means of linear mixed models (LMMs) using the *lme* function of the *nlme* package (Pinheiro *et al.* 2017). In these analyses, bird identity was included as a random factor and the presence/absence of a ring on both tarsi was included as a fixed factor. The significance of the fixed factor was tested by comparing the model with and without it using the function *anova* of the *stats* package (R Core Team 2019). In these analyses, values are reported as means $\pm$ sd and differences are considered significant at $P < 0.05$.

To test the hypothesis that the presence of leg rings affects intra-dive parameters (i.e. VeDBA, foot stroke frequency and amplitude, pitch angle and rate of change of depth during the descent), we employed LMMs. In these models, the explanatory variables were: presence/absence of a ring on both tarsi, maximum dive depth, instantaneous depth (linear, quadratic and/or ln term), the interaction between instantaneous depth and the presence/absence of a ring on both tarsi, and bird mass. Maximum depth reached during a dive was included in the models because this can affect the descent angle (Ropert-Coudert *et al.* 2005), and instantaneous depth was included because energy expenditure decreases with depth (Wilson *et al.* 1992, Cook *et al.* 2008, 2010). The interaction between instantaneous depth and ring was included because, during the descent phase of a dive, the force of buoyancy decreases with depth and birds adjust their locomotor activity correspondingly (Wilson *et al.* 2006, Cook *et al.* 2010). Body mass was included in the models due to the effect it has on diving behaviour (Schreer & Kovacs 1997). In all models, we included descent dive phase nested within each individual as a random factor. Foot stroke parameters were averaged over 5-m bins in order to have several depth categories and at the same time several points in each depth category. Smaller bins (e.g. 2 m) would contain very few points, whereas larger bins (e.g. 10-m bins) would generate only three depth categories for females and four categories for males, with the additional problem that the first category would only contain data from 5 to 10 m depth (due to an inability to resolve the high frequency of strokes over the first 5 m of the water column, see above). Finally, to measure the overall efficiency of ringed vs. unringed birds, the descent rate per unit VeDBA was calculated. For this, for both sexes, the fitted values from the best model (see below) explaining the relationship between descent rate and the previously mentioned explanatory variables were divided by the fitted values from the best model explaining the relationship between VeDBA and the same explanatory variables. Once this had been done, we constructed two models (one for females and one for males) where the response variable was the overall efficiency and the explanatory fixed variables and the random factor structure were the same as in the rest of the models.

The performance of the global model for each response variable was compared with that of

simpler candidate models that exclude one or more predictors using the Akaike information criterion (AIC) (Burnham & Anderson 2002). The AIC and the AIC weight (w_i) for each model, as well as the ΔAIC values between models, were obtained using the *nlme* and *MuMin* packages (Bartoń 2019). Models were ranked according to their ΔAIC values, and the model with the lowest ΔAIC was chosen as the best to explain each response variable (Burnham & Anderson 2002). However, if several competing models were ranked within ΔAIC ≤ 4 of the best ranked model, the most parsimonious model (i.e. the one that included the fewest uninformative parameters) was selected as the best model for inference (Lehikoinen *et al.* 2021). A parameter was considered uninformative if the 85% confidence interval (CI) included zero (Arnold 2010). As our model set included interaction terms, we did not model average parameter estimates (Cade 2015).

RESULTS

Instrumented birds performed a total of 4057 dives and general diving parameters did not differ between ringed and unringed Shags (Table 1). Both females and males carrying rings performed the same mean number of dives per foraging trip as Shags without rings and no differences between ringed and unringed birds were observed, either in total dive duration or in the mean amount of time birds allocated to each dive phase (Table 1). The mean maximum depth and the mean descent rate were also similar between ringed and unringed Shags (Table 1).

Of the total recorded dives, 2929 met the conditions required for further analyses (see Methods). Of these dives, 951 and 1144 were performed by ringed and unringed females, respectively. The number of dives performed by ringed males was 389 and by unringed males was 445. For both sexes, the best model explaining the variation in VeDBA during the descent phase included instantaneous depth, maximum dive depth, and the interaction between depth and ring ($w_i = 0.723$ for females and $w_i = 0.571$ for males; Table 2). As indicated by the high parameter likelihood values and 85% confidence interval (CI) excluding zero, for both male and female Imperial Shags, VeDBA decreased with instantaneous depth following a curvilinear relationship (Fig. 1a,b, Table S1). However, the relationship between VeDBA and

Table 1. Summary statistics (mean ± sd) from diving records of 20 unringed (10 females and 10 males) and 20 ringed (10 females and 10 males) Imperial Shags breeding at Punta León colony, Argentina.

Sex	Condition	Instrumented animals	Dives (n)	Dive duration (s)	Descent duration (s)	Bottom duration (s)	Ascent duration (s)	Maximum depth (m)	Descent rate (m/s)
Females	Unringed	10	120.60 ± 47.54	108.41 ± 16.16	18.54 ± 2.62	74.49 ± 12.33	15.38 ± 2.39	26.37 ± 3.42	1.38 ± 0.06
	Ringed	10	119.10 ± 54.34	101.66 ± 19.24	17.74 ± 2.33	68.61 ± 16.32	15.32 ± 2.16	25.17 ± 4.04	1.36 ± 0.12
	Statistics		W = 47.0	L ratio = 0.776	L ratio = 0.550	L ratio = 0.896	L ratio = 0.002	L ratio = 0.547	L ratio = 0.336
	P value		P = 0.850	P = 0.378	P = 0.458	P = 0.344	P = 0.963	P = 0.460	P = 0.562
Males	Unringed	10	86.0 ± 34.59	81.98 ± 34.26	18.77 ± 5.49	46.14 ± 24.96	17.08 ± 5.83	25.59 ± 10.43	1.20 ± 0.28
	Ringed	10	80.0 ± 43.33	88.72 ± 42.82	22.01 ± 8.11	46.79 ± 28.01	19.92 ± 7.39	28.47 ± 13.48	1.10 ± 0.30
	Statistics		W = 45.50	L ratio = 0.157	L ratio = 1.140	L ratio = 0.002	L ratio = 0.952	L ratio = 0.298	L ratio = 0.566
	P-value		P = 0.761	P = 0.692	P = 0.285	P = 0.963	P = 0.329	P = 0.585	P = 0.452

Table 2. Top models (ΔAIC < 4) explaining the relationship between (a) energy expenditure (VeDBA), (b) peak frequency and (c) peak amplitude, and presence/absence of a ring on both tarsi (Ring), maximum depth (Max Depth), instantaneous depth (Depth), the interaction between instantaneous depth and the presence/absence of a ring on both tarsi (Depth : Ring), and body mass (Body Mass) of female and male Imperial Shags. Best models for inference are in bold. The number of parameters (k), AIC difference from the top model (ΔAIC) and Akaike weights (w_i) are reported. See Methods for details.

Response variable	Females				Males			
	Fixed effects	k	ΔAIC	w_i	Fixed effects	k	ΔAIC	w_i
(a) VEDBA	**Depth + Depth^2 + Max Depth + Ring + Depth : Ring + Depth^2 : Ring**	**10**	**0.000**	**0.723**	**Depth + Depth^2 + Max Depth + Ring + Depth : Ring + Depth^2 : Ring**	**10**	**0.000**	**0.571**
	Depth + Depth^2 + Max Depth + Ring + Depth : Ring + Depth^2 : Ring + Body Mass	11	1.910	0.277	Depth + Depth^2 + Max Depth + Ring + Depth : Ring + Depth^2 : Ring + Body Mass	11	0.570	0.429
(b) Peak frequency	**Depth + Max Depth + Ring + Depth : Ring**	**14**	**0.000**	**0.629**	Depth + Max Depth + Ring	13	0.000	0.297
	Depth + Max Depth + Ring + Body Mass + Depth : Ring	15	1.630	0.279	Depth + Max Depth + Body Mass	13	0.450	0.238
					Depth + Max Depth	**12**	**0.580**	**0.223**
					Depth + Max Depth + Ring + Body Mass	14	0.930	0.186
(c) Peak amplitude	**Depth + Max Depth + Ring + Body Mass + Depth : Ring**	**15**	**0.000**	**0.505**	**Depth + Max Depth + Ring + Depth : Ring**	**20**	**0.000**	**0.420**
	Depth + Max Depth + Ring + Depth : Ring	14	0.220	0.453	Depth + Ring + Depth : Ring	19	0.700	0.296
					Depth + Max Depth + Ring + Body Mass + Depth : Ring	21	1.860	0.166
					Depth + Ring + Body Mass + Depth : Ring	20	2.540	0.118

instantaneous depth differed between ringed and unringed birds. In the case of females, VeDBA was higher for ringed than for unringed birds, principally between 10 and 20 m depth (Fig. 1a). For males, VeDBA was similar between both conditions except below 35 m, where VeDBA was higher for unringed birds (Fig. 1b). Descent phase VeDBA was also affected by the maximum depth reached during a dive; for females, the deeper they ultimately dived, the lower the relative VeDBA, whereas for males the opposite pattern was observed (Table S1).

Below 5 m depth, the best model explaining the variation in the frequency of foot strokes (i.e. peak frequency) during the descent phase of female Shags included instantaneous depth, maximum depth, and the interaction between depth and the presence of rings (w_i = 0.629; Table 2). The frequency of foot strokes was positively affected by the maximum depth reached during a dive, decreased as females swam deeper, and was similar for ringed and unringed females between 5 and 20 m. However, the frequency of

foot strokes was higher for females carrying rings for depths below 20 m (Fig. 2a, Table S1). In the case of males, there was substantial uncertainty in model selection (there were several models with ΔAIC$_c$ ≤ 4; Table 2). The most parsimonious model (w_i = 0.223) showed that for males, the frequency of foot strokes was not affected by the presence of rings, decreased as birds swam deeper, and was positively affected by the maximum depth reached during a dive (Fig. 2b, Table S1).

For both sexes, the best model explaining the variation in peak amplitude during the descent phase of a dive included instantaneous depth, maximum depth, ring, and the interaction between ring and depth (w_i = 0.505 and w_i = 0.420 for females and males, respectively; Table 2). In the case of females, the best model also included body mass (Table 2). For females, the depth-corrected peak amplitude was higher in ringed than in unringed birds, principally during the first 20 m of the descent phase, where the foot stroke amplitude of ringed birds was almost 10%
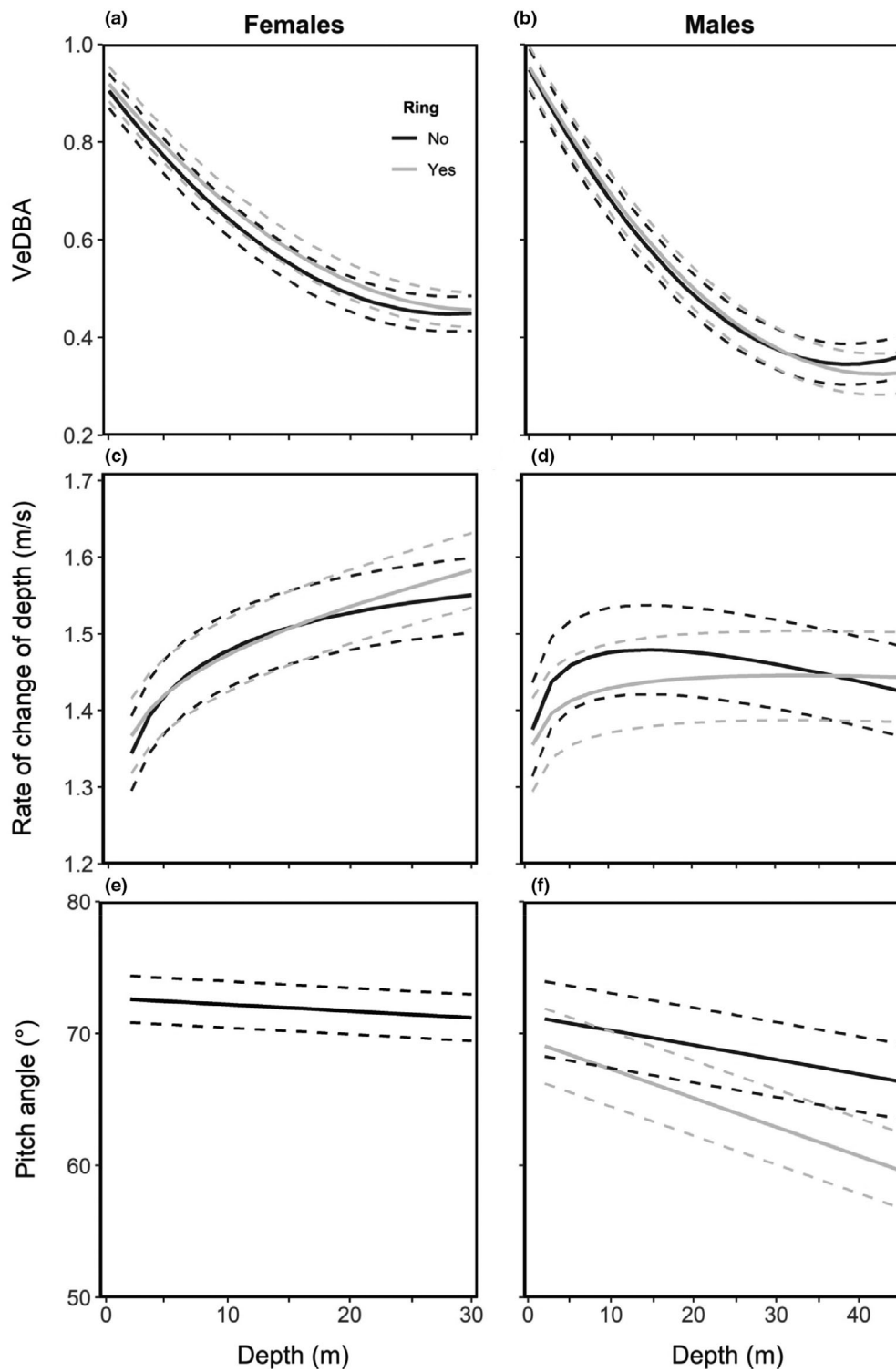
Figure 1. VeDBA (a, b), rate of change of depth (c, d) and pitch angle (e, f) in relation to instantaneous depth during the descent phase of ringed and unringed female and male Imperial Shags. For both sexes, the line represents the fitted values obtained from the estimated parameters of the best model and the dashed lines represent the 95% CI. In (e) only one line and its 95% CI is shown, as the parameter Ring was not included in the best model.
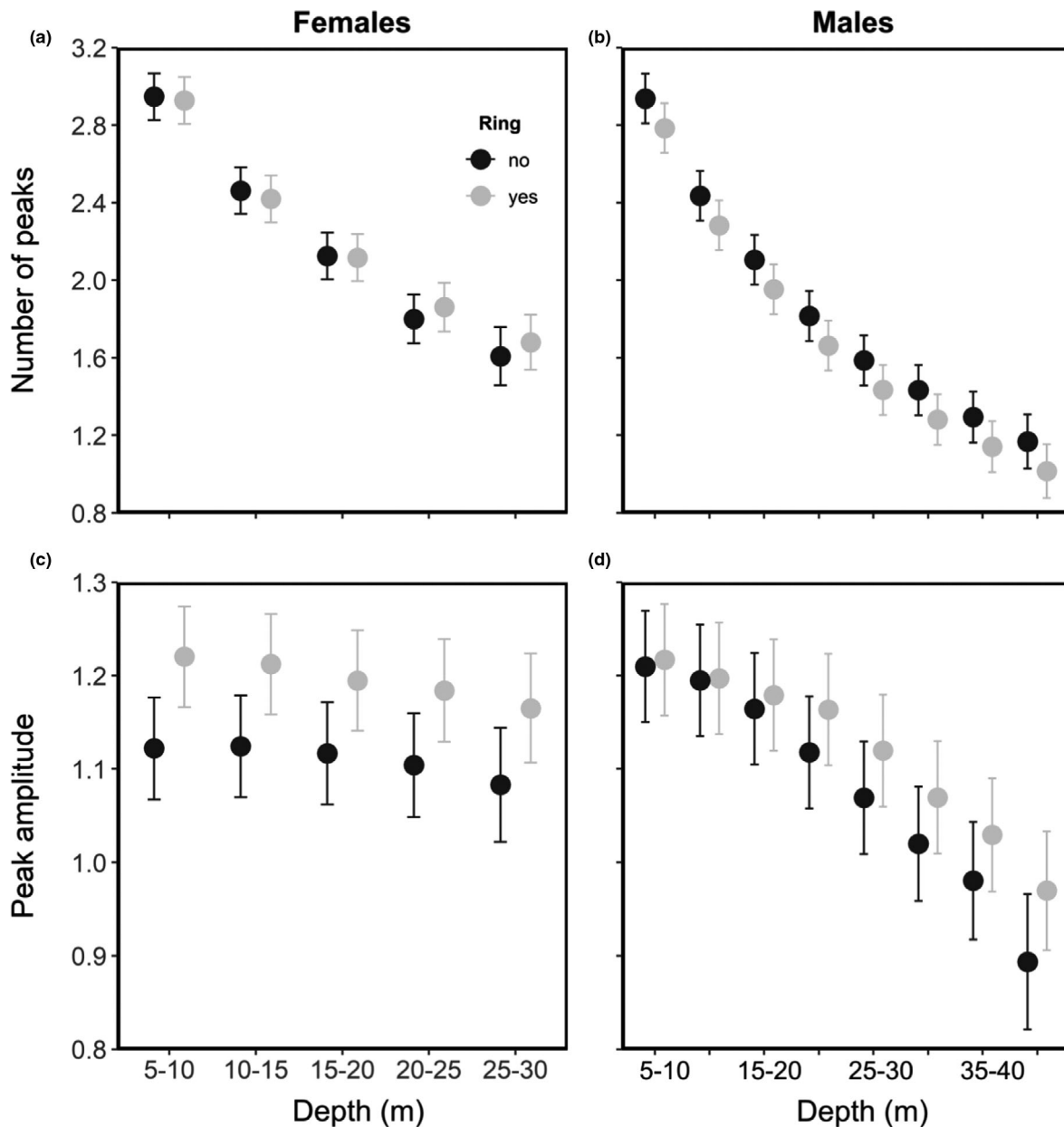
Figure 2. Foot kick frequency (a, b) and peak amplitude (c, d) at different instantaneous depths (represented by 5-m bins) in the descent diving phase of female and male Imperial Shags. Fitted values were obtained from the estimated parameters of the best model. Points represent the mean while error bars represent 95% CI.

higher than that of unringed birds (Fig. 2c, Table S1). In males, the average foot stroke amplitude was also higher for ringed birds and, within each depth bin, differences were greater below 20 m depth (Fig. 2d, Table S1).

During the descent, the rate of change of depth ranged between 0.5 and 2.37 m/s. For females, the best model explaining the variation in the rate

of change of depth during the descent included instantaneous depth (linear and ln terms), maximum depth and the interaction between instantaneous depth (both linear and ln term) and ring ($w_i = 0.479$; Table 3). As females descended deeper, the rate of change of depth increased similarly for both ringed and unringed animals, but females carrying rings descended more quickly at

depths below 15 m (Fig. 1c, Table S2). For males, the best model explaining the variation in the rate of change of depth also included instantaneous depth (both terms), maximum depth, ring, and the interaction between depth and ring ($w_i = 0.697$; Table 3). Males without rings descended the water column faster than birds with rings and this difference was most obvious between 5 and 20 m depth (Fig. 1d, Table S2).

Table 3. Top models (ΔAIC < 4) explaining the relationship between (a) rate of change of depth, (b) pitch angle and (c) overall efficiency, and presence/absence of a ring in both tarsi (Ring), maximum depth (Max Depth), instantaneous depth (Depth), the interaction between instantaneous depth and the presence/absence of a ring on both tarsi (Depth : Ring), and body mass (Body Mass) of female and male Imperial Shags. Best models for inference are in bold. The number of parameters (k), AIC difference from the top model (ΔAIC) and Akaike weights (w_i) are reported. See Methods for details.

Response variable	Females				Males			
	Fixed effects	k	ΔAIC	w_i	Fixed effects	k	ΔAIC	w_i
(a) Rate of change of depth	**Depth + ln (Depth) + Max Depth + Ring + Depth : Ring + ln (Depth) : Ring**	**10**	**0.000**	**0.479**	**Depth + ln (Depth) + Max Depth + Ring + Depth : Ring + ln (Depth) : Ring**	**10**	**0.000**	**0.697**
	Depth + ln (Depth) + Max Depth + Ring + Body Mass + Depth : Ring + ln (Depth) : Ring	11	0.290	0.415	Depth + ln (Depth) + Max Depth + Ring + Body Mass + Depth : Ring + ln (Depth) : Ring	11	2.000	0.257
(b) Pitch angle	**Depth**	**5**	**0.000**	**0.184**	**Depth + Max Depth + Ring + Depth : Ring**	**8**	**0.000**	**0.537**
	Depth + Body Mass	6	0.610	0.136	Depth + Max Depth + Ring + Body Mass + Depth : Ring	9	0.290	0.463
	Depth + Max Depth	6	1.050	0.109				
	Depth + Ring	6	1.600	0.083				
	Depth + Max Depth + Body Mass	7	1.670	0.080				
	Depth + Ring + Body Mass	7	1.680	0.079				
	Depth + Ring + Depth : Ring	7	1.780	0.076				
	Depth + Ring + Body Mass + Depth : Ring	8	1.870	0.072				
	Depth + Max Depth + Ring	7	2.660	0.049				
	Depth + Max Depth + Ring + Body Mass	8	2.760	0.046				
	Depth + Max Depth + Ring + Depth : Ring	8	2.850	0.044				
	Depth + Max Depth + Body Mass + Ring + Depth : Ring	9	2.960	0.042				
(c) Overall efficiency	**Depth + Depth² + Max Depth + Ring + Body Mass + Depth : Ring + Depth² : Ring**	**11**	**0.000**	**0.543**	**Depth + Depth² + Max Depth + Ring + Depth : Ring + Depth² : Ring**	**10**	**0.000**	**0.634**
	Depth + Depth² + Max Depth + Ring + Depth : Ring + Depth² : Ring	10	0.380	0.449	Depth + Depth² + Max Depth + Ring + Body Mass + Depth : Ring + Depth² : Ring	11	1.100	0.366

Finally, for females, even though there was substantial uncertainty in model selection, the best model describing the variation in the pitch descent angle included only instantaneous depth ($w_i = 0.184$; Table 3). Females' descent pitch angle decreased as they descended deeper (Fig. 1e). In the case of males, the best model explaining the variation in the descent pitch angle included instantaneous depth, maximum depth, ring, and the interaction between depth and ring ($w_i = 0.537$; Table 3). Male descent pitch angle was always higher for animals without rings than for animals carrying rings (Fig. 1f, Table S2).

DISCUSSION

As far as we know, this is the first study that has considered the effect of carrying leg rings on the performance of a foot-propelled diving bird at within-dive scales. This is important because diving animals can compensate for inefficiencies that may be caused by external tags, such as increased drag, apparently maintaining overall dive efficiency (e.g. dive duration and inter-dive surface pauses) by accruing O_2 deficit and CO_2 build-up over multiple dives (Cornick *et al.* 2006, Ropert-Coudert *et al.* 2007). Importantly, therefore, we examine changes in movement performance where effects, if any, are likely to be less well concealed. In a general sense, the performance parameters of both ringed and unringed bird groups followed what was expected: using VeDBA as a proxy for energy expenditure (Qasem *et al.* 2012), Imperial Shag descent phase VeDBA varied in a curvilinear manner with instantaneous depth and maximum depth. This relationship stems from the inverse relationship between depth and buoyancy (Wilson *et al.* 1992, Cook *et al.* 2008, 2010) because Imperial Shags have an appreciable amount of air in their feathers (Wilson *et al.* 1992, Grémillet *et al.* 2005, Quintana *et al.* 2007) and inhale before diving (Quintana *et al.* 2007) so that birds are substantially buoyant (Wilson *et al.* 1992, Watanuki *et al.* 2003, Wilson & Quintana 2004). However, following Boyle's Law, this buoyancy decreases with increasing depth (Wilson *et al.* 1992, Watanuki *et al.* 2003, Wilson & Quintana 2004). Thus, birds have to invest power to overcome the buoyancy force in relation to depth (Fig. 1a,b) as well as invest power to overcome drag if descent rates are to be maintained approximately constant (between 1.4 and 1.6 m/s; Fig. 1c,d). All this agrees with

data reported by Watanuki *et al.* 2005 for the European Shag *Phalacrocorax aristotelis* that birds adjust average forward thrust via both stroke frequency and stroke force, both reducing with depth.

However, assuming that VeDBA is a suitable proxy for the rate of energy expenditure, the investment of power to descend was apparently not the same between ringed and unringed birds. This seems to be due to increased stride amplitude in males for some depths and across all depths in females, indicating that both ringed sexes worked harder against drag (or the propulsive mechanism was less efficient) compared with unringed birds for similar rates of change of depth. In fact, ringed females did show an increased descent rate at depths exceeding 15 m that might, in part, explain the higher VeDBA at these depths, although this does not account for the shallower depth performance. Conversely, despite the higher VeDBA for descent in ringed males, they descended less quickly than unringed birds, partly perhaps because their descent angle was shallower (Fig. 1e,f). The different responses to carrying a ring on both tarsi between females and males could be associated with the intersexual differences in body mass, which are likely to affect diving behaviour (Quintana *et al.* 2011, Gómez Laich *et al.* 2012). In addition, differences between sexes could be associated with the different plasticity both sexes have in their foraging behaviour (Quillfeldt *et al.* 2011, Harris *et al.* 2014). Females have been observed to be more efficient than males when diving to depths shallower than 30 m (Gómez Laich *et al.* 2012), exploiting a narrower depth range and exhibiting a higher degree of behavioural consistency (Quillfeldt *et al.* 2011, Harris *et al.* 2014). Whatever the mechanism by which rings affect propulsion, for the shallower diving and more consistent sex (i.e. females), the best solution seems to be to maintain the body pitch angle and descent rate, though this necessitates a variable kick amplitude (i.e. foot stroke force). Conversely, the deeper- and less consistently diving males seem to adopt a different strategy which involves modifying both the descent angle and the descent rate.

Given that there is presumably strong selection pressure for these bottom-feeding Shags (Shepard *et al.* 2010, Gómez-Laich *et al.* 2015) to descend the water column as efficiently as possible, we can examine overall efficiency in ringed vs. unringed birds by combining terms to look at descent rate
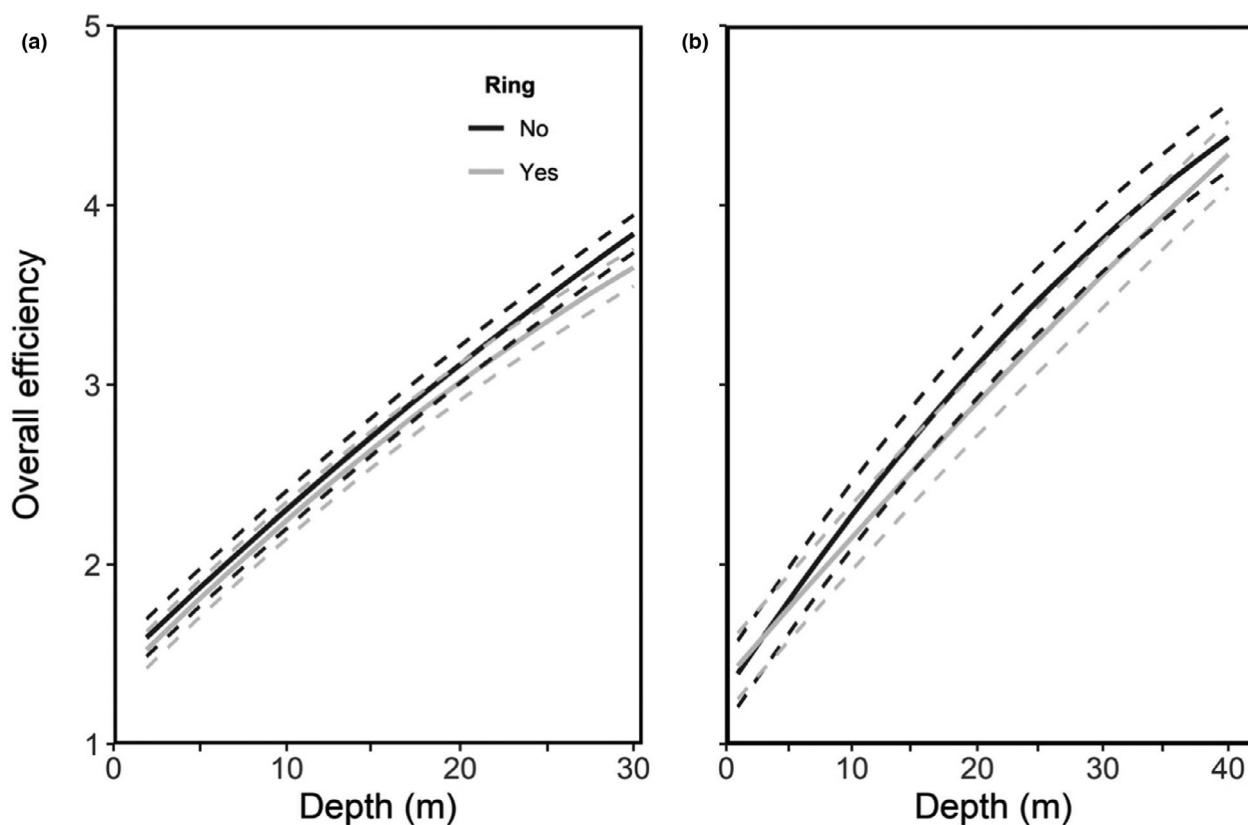
Figure 3. Overall efficiency (measured as the descent rate per unit VeDBA) in relation to instantaneous depth for female (a) and male (b) Imperial Shags. For both sexes, the line represents the fitted values obtained from the estimated parameters of the best model and the dashed lines represent the 95% CI.

per unit VeDBA invested (Fig. 3, Table S2). This approach essentially combines all performance terms and power metrics across the depths and shows clearly that our ringed birds worked harder for a given output than unringed birds by about 3.5% for females and 4.3% for males across all depths. Why is this? The explanation proposed for higher energy expenditure (measured directly) for ringed penguins (Culik *et al.* 1993) was grounded in presumed increases in drag, not least because the rings are located half-way along the body and can induce flow separation at that point (*cf.* Bannasch *et al.* 1994). A similar phenomenon was reported by Pennycuik *et al.* (2012) for flying birds. Increased drag is less easy to understand in the cormorants because the rings are attached to the far posterior end of the body and thus flow separation would occur behind the bird. However, the rings are attached to the propulsion apparatus and so may well decrease the efficiency of the feet in propelling water backwards. Studies

using techniques such as digital particle image velocimetry to examine flow patterns (*cf.* Drucker & Lauder, 1999) may provide a more specific answer.

Whatever the precise mechanism, the issue of decreased foraging efficiency due to the rings must be taken seriously, not least because such rings are effectively permanent, and therefore detrimental effects, however small, may cause more substantial longer-term detriment. This effect was highlighted by Saraux *et al.* (2011), who found that ostensibly trivially small flipper rings in King Penguins *Aptenodytes patagonicus* attached over years affected population processes. Our study is based on few birds, and the effect is relatively small, and likely to be even smaller when birds are foraging along the seabed because their investment in propulsion is much reduced (Gómez-Laich *et al.* 2013) and where prey are caught primarily by the birds using their highly mobile necks (White *et al.* 2007, Gómez-Laich *et al.* 2015, Wilson *et al.* 2017).

However, we note that, as modelled by Pennycuik *et al.* (2012) and demonstrated by Saraux *et al.* (2011), even small tags attached to animals can result in large differences in detriment over time. This may be particularly germane given that natural selection is considered to act on small differences (Orr 2005). Future studies recording acceleration at a higher sampling rate should tell us whether rings have a stronger effect during the first metres of the water column where the upthrust force is maximal and consequently the rate of energy expenditure is greatest (Wilson *et al.* 1992). Unfortunately, our study focused on analysing the effect of carrying a ring on both tarsi, so we cannot rule out whether what we observed is a consequence of the presence of one ring or an additive effect caused by the presence of two rings. Finally, our study focused on the diving behaviour of adults in a small time window: the early chick rearing period. Although we do not expect rings to cause a reduction in breeding success, even in years of low prey availability, we would advocate further studies to consider potential discrete and cumulative effects of attaching rings on birds before ringing programmes are initiated.

AUTHOR CONTRIBUTIONS

Agustina Gómez-Laich: Conceptualization (equal); Formal analysis (equal); Investigation (lead); Methodology (equal); Supervision (equal); Writing-original draft (lead); Writing-review & editing (equal). **Carolina Pantano:** Formal analysis (equal); Writing-original draft (equal). **Rory P. Wilson:** Conceptualization (equal); Investigation (equal); Supervision (equal); Writing-review & editing (equal). **Walter S. Svagelj:** Formal analysis (supporting); Methodology (supporting). **Ken Yoda:** Funding acquisition (equal); Resources (equal). **Richard Gunner:** Formal analysis (supporting). **Flavio Quintana:** Conceptualization (lead); Funding acquisition (equal); Investigation (equal); Methodology (equal); Resources (equal); Supervision (equal); Writing-review & editing (equal).

Data availability statement

Data are available on request from the corresponding author.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Coefficient estimates of the best model describing the variation in (a) energy expenditure (VeDBA), (b) peak frequency and (c) peak amplitude.

Table S2. Coefficient estimates of the best model describing the variation in (a) rate of change of depth, (b) pitch angle and (c) overall efficiency.