

Flipper beat frequency and amplitude changes in diving green turtles, *Chelonia mydas*

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Received: 29 November 2005 / Accepted: 13 June 2006 / Published online: 29 July 2006
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Abstract Using a turtle-borne camera system, changing flipper beat frequency and amplitude were measured in five diving green turtles (*Chelonia mydas* Linnaeus 1758) in the Bahía de los Angeles, Mexico (28°58'N, 113°33'W). These observations were made between June and August 2002. Turtles worked hardest (i.e., had the highest flipper beat frequency and amplitude) at the start of descents when positive buoyancy is predicted to oppose their forward motion. During the later part of descents, turtles worked less hard in line with opposing buoyancy forces being reduced. For example, flipper beat frequency declined from about 60–80 beats min⁻¹ at the start of descent to around 25–40 beats min⁻¹ after 30 s of the descent. At the start of ascents the flipper beat frequency was around 30 beats min⁻¹, lower than on descent, and declined as the ascent progressed with often passive gliding for the final few meters to the surface. This pattern of effort during diving appears to apply across a range of marine reptiles, birds and mammals suggest-

ing that graded effort during descent and ascent is an optimum solution to minimising the cost of transport during diving.

Introduction

Buoyancy has strong implications for the diving behaviour of many air-breathing diving animals. At the start of dives most divers are positively buoyant due to air in the lungs and, in the case of birds, air trapped in the plumage. As the descent progresses these air-filled spaces are compressed due to increasing pressure resulting in less positive buoyancy until, if dives are deep enough, neutral and then negative buoyancy is attained (Wilson et al. 1992; Skrovan et al. 1999; Williams et al. 2000). For example, it has been estimated that diving sperm whales (*Physeter macrocephalus*) attain neutral buoyancy at a great depth, 250–850 m (Miller et al. 2004), presumably due to high amounts of stored lipid. In contrast, Brunnich's guillemots (*Uria lomvia*) are estimated to attain neutral buoyancy around 70 m (Lovvorn et al. 2004), while for adult green turtles (*Chelonia mydas*) it has been estimated that the maximum depth at which neutral buoyancy can be attained is considerably shallower, around 15–20 m (Hays et al. 2004a), probably due to the weight of the carapace. Conversely when these divers ascend at the end of a dive, initially they may have to overcome negative buoyancy and then as the ascent continues and air-filled spaces expand due to reduced pressure, so buoyancy increases and may aid the diver's ascent.

In line with these predictable changes in buoyancy, it is well known that both diving mammals and birds change their swimming effort during dives. For example,

Communicated by J.P. Grassle, New Brunswick

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Williams et al. (2000) noted a consistent transition from active flipper beating to passive gliding during descent for a number of marine mammal species. Such findings have since been extended to other marine mammals as well as diving birds (e.g., Miller et al. 2004; Hooker et al. 2005). In addition to this dichotomy between active swimming and passive gliding, second-by-second modifications in diving behaviour, paralleling buoyancy changes, have also been observed in diving birds (penguins and guillemots) (van Dam et al. 2002; Watanuki et al. 2003; Lovvorn et al. 2004). Similarly, previous observations on one green turtle showed a continuous decrease in flipper beat frequency during dives (Hays et al. 2004b). These studies suggest that interactions between dive effort and buoyancy may apply across a range of diving mammals, birds and reptiles, although details for reptiles remain scant.

To improve our understanding of swimming effort during turtle diving, we used a turtle-borne camera system (Critttercam, Marshall 1998). This camera system was used to record flipper beat frequency in sea turtles by Reina et al. (2005). In this pioneering study flipper beat frequency was measured by a forward pointing Critttercam attached to leatherback turtles (*Dermochelys coriacea*) (Reina et al. 2005). Here we build on the ideas developed by Reina et al. (2005) to examine flipper beat frequency and amplitude in diving green turtles, which together, effectively reflect swimming effort.

Materials and methods

Study site and *Chelonia mydas* (Linnaeus 1758)

The study was conducted at Bahía de los Angeles (28°58'N, 113°33'W), on the western coast of the Baja California Peninsula, Mexico between June and August 2002. This is a year-round foraging area for both immature and adult green turtles, where turtles feed on marine macroalgae in water depths to 40 m. As part of a long-term demographic study, we captured green turtles along nearshore margins of the feeding area using large-mesh entanglement nets (Seminoff et al. 2003). Upon capture, turtles were transported by boat for 1–4 km to the Archelon Research Station for processing and Critttercam attachment. During transport a damp towel was placed over each turtle to keep them cool. Equipped turtles were released within 24 h at or near (within 0.5 km) the site of initial capture after being maintained in cool conditions throughout their time in captivity. They showed no adverse signs of capture and all the attached equipment was removed within a few days (see below). Turtles were weighed

with a spring balance and their curved carapace length (CCL) measured with a flexible tape.

Critttercam technology

Critttercam includes a video camera integrated with a time-depth recorder (TDR) and on-board microcomputer (up to 512 KB of memory) that allows data collection intervals to be programmed (Marshall 1998). Water depth and temperature information was collected continuously at 2–7 s intervals during each deployment (up to 1 day). The Critttercam had a Hi-8 video camera; video configurations included both short-play (3 h) and long-play (6 h) and were programmed to record video continuously or at a user-defined duty cycle. Video footage was stored on analogue cassettes for subsequent playback on a standard VCR. These components are housed in a tubular aluminum cylinder (10.1 cm diameter, 31.7 cm in length) that has a hydrodynamically optimized dome and conical tail portion composed of incompressible syntactic foam designed to minimize drag. Units weighed 2 kg out of water (< 4% of turtle body weight), but were neutrally buoyant in water due to a counter-weighting system (see below).

The Critttercam was attached at the peak of the dome of the carapace. We used a dual plate attachment system consisting of a top plate linked to the Critttercam with two 10 cm diameter hose clamps and a bottom plate adhered to the carapace with a nylon mesh apron and 5 min quick-set epoxy. The bottom plate was counter-weighted to achieve neutral buoyancy in water. The anterior portions of the top and bottom plates were interlocked by a screw-and-groove assembly and the posterior portions of the plates were connected with a burn-wire assembly and backup corrosive (Mg) link. Upon burn wire ignition or corrosion of the backup link, the two plates disengaged. The slightly positively buoyant camera floated to the surface. Captive trials and one recapture of a wild turtle demonstrated that base plates were shed from the carapace within 10 days of camera detachment.

Cameras were programmed to detach 4–20 h after the turtles were released. Units were recovered with the aid of integrated very high frequency (VHF) radio (MOD 050, Telonics Inc., Mesa, Arizona) and sonic transmitters (CHP-87-L, Sonotronics, Tucson, Arizona). Radio and acoustic transmissions were tracked using a TR-4 VHF receiver (Telonics) with a three-element Yagi antenna and VR-60 acoustic receiver (Vemco Ltd., Shad Bay, Nova Scotia) with V-10 directional hydrophone (Vemco Ltd.), respectively. The maximum reception range of VHF transmissions was

up to 14 km in open areas while that of acoustic transmitters was ~ 2 km.

The Crittercam pointed forward on the carapace. We selected 5 deployments from a total of 36 where at least one flipper could be clearly seen when the turtle was swimming. This depended on the exact positioning and angle of the mounted Crittercam. We limited our sample size to five individuals simply because of the time constraints involved in analyzing the video tapes (see below). Video images were analyzed using a standard VCR and the timing of each flipper beat was recorded using event software (Hindsight for MS-DOS). This involved pressing a key of a PC each time a flipper beat occurred, with the event software recording the timing of each key stroke. The flipper beat frequency was then calculated from the interval between consecutive flipper beats up to a maximum beat-beat interval of 30 s beyond which we defined the turtle as passively gliding. All video analysis was done by one person (GCH) to remove inter-observer variation, with replicate measurements of individual dives confirming consistency in the video analysis technique. We qualitatively recorded the flipper beat amplitude by direct observation of the VCR images. We viewed every dive and made qualitative observations to confirm that the same pattern was happening on all dives. To make quantitative measurements of beat amplitude was very time consuming as the video was viewed frame-by-frame (30 frames s^{-1}). Therefore we picked a random selection of dives for this frame-by-frame analysis. Again all this video analysis was done by one person (GCH). We selected a point on the side of the head just behind the eye as a reference and then measured the closest distance that the flipper approached this point in each beat cycle. This distance was then divided by the width of the head to produce the index of amplitude for each beat (see Fig. 1).

Results

We recorded the pattern of flipper beating on 78 dives for 5 free-living green turtles (*Chelonia mydas*). The maximum depth of these dives ranged from 6.0 to 37.1 m and the duration from 1.1 to 17.7 min (Table 1). We were readily able to identify clear stroking patterns within dives as illustrated in Fig. 2, which shows the beat frequency recorded during one entire dive. Dives typically involved descent to the seabed, whereupon the turtle returned straight to the surface, traveled along the seabed, or traveled in mid-water as if trying to move to another site. However, feeding was not observed during any dives so we conclude that dives

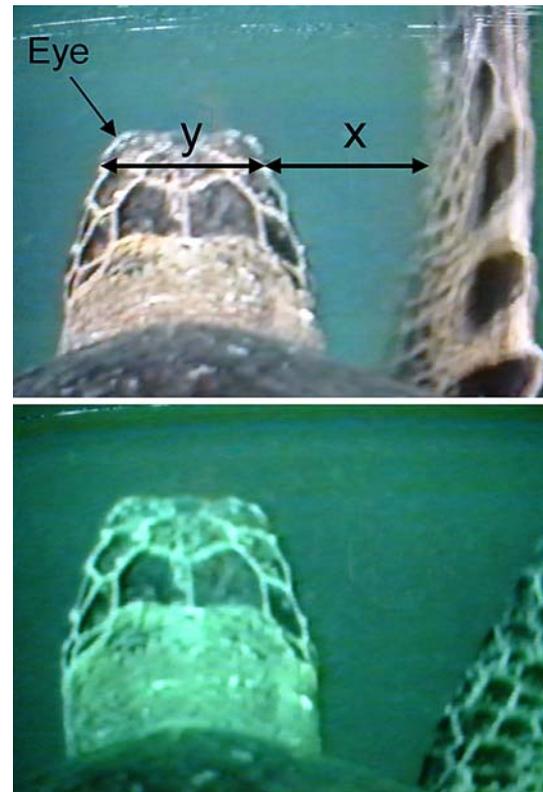


Fig. 1 *Chelonia mydas*. Single frames from the Crittercam showing the right flipper of turtle 1. *Upper panel* A large amplitude flipper beat; *lower panel* a small amplitude flipper beat. Change in water color (bluish to more greenish) reflects that small amplitude beats occur deeper. To measure the relative change in flipper beat amplitude, we selected a point on the side of the head as a reference and then measured the closest the flipper approached this point in each beat cycle (x). This distance was then divided by the width of the head (y) to produce the index of amplitude for each beat which decreased with beat amplitude ($0 - x/y$)

had an exploratory and/or traveling function. Visibility was only a few meters and during the final few seconds before reaching the seabed the turtles seemed to adjust their descent angle to make a “controlled landing”. For all dives the flipper beat frequency decreased as the descent progressed. Typically beat frequency dropped by about 50% during the first 20 s of each dive, from around $60\text{--}80 \text{ beats min}^{-1}$ down to $25\text{--}40 \text{ beats min}^{-1}$ (Fig. 3). Despite these same general patterns within descents, individuals differed in their absolute beat frequencies. For example, turtle 4 consistently had a very high initial beat frequency (Fig. 3 and Table 1).

In addition, we recorded this same universal pattern for flipper beat amplitude: amplitude was always initially large and then decreased as the descent continued (Fig. 5). On ascent the flipper beat frequency was lower than on descent, being around $30 \text{ beats min}^{-1}$ at the start of each ascent (Fig. 4). Over the course of the ascent to the surface there were systematic declines in

Table 1 *Chelonia mydas*. For each turtle a summary of the dives performed. Means \pm SD are shown

Turtle id	CCL (cm)	Weight (kg)	Dives	Temperature ($^{\circ}$ C)	Duration (min)	Mean max depth (m)	Max depth ($n \text{ min}^{-1}$)	FBF start ($n \text{ min}^{-1}$)	FBF end ($n \text{ min}^{-1}$)
1	86.6	79.5	18	24.4 (0.4)	4.5 (1.2)	20.5 (4.5)	27.4	54.0 (4.4)	32.0 (2.0)
2	87.3	75.0	13	25.9 (0.3)	8.6 (2.9)	11.1 (7.3)	28.9	44.2 (5.1)	23.0 (1.8)
3	76.4	56.8	18	26.0 (0.6)	6.5 (1.7)	23.3 (9.9)	35.2	40.1 (4.9)	25.9 (2.1)
4	69.5	38.6	11	25.4 (0.8)	12.9 (3.8)	29.8 (3.4)	33.6	72.5 (4.8)	37.8 (2.9)
5	93.4	107.7	18	25.3 (0.6)	5.8 (2.6)	24.0 (6.9)	37.1	57.3 (4.6)	26.4 (1.7)

Mean maximum depth represents mean of all maximum depths recorded by that turtle. CCL = curved carapace length, flipper beat frequency (FBF) at the start and end of the first 20 s of dives is also shown. In each case the mean of the first three measurements and last three measurements for each dive were calculated respectively

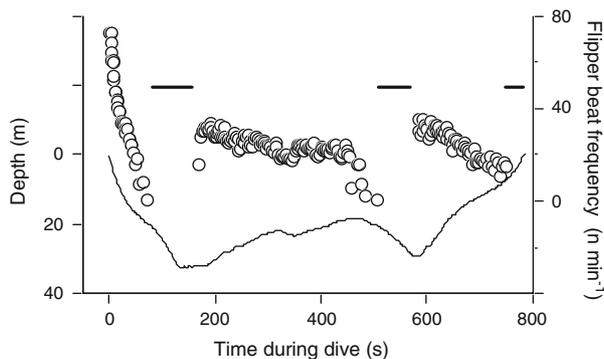


Fig. 2 *Chelonia mydas*. Flipper beat frequency and dive depth during one complete dive of turtle 1 illustrating reduction in beat frequency during initial descent and passive (i.e., no flipper beats) descent during deep (> 20 m) parts of dive. Also evident is reduction in flipper beat frequency during final ascent to the surface. An absence of points for flipper beat frequency indicates periods of passive gliding and these periods are indicated by horizontal black bars. Solid line shows depth data and open circles show flipper beat frequency

beat frequency and, as the ascent progressed, often there was passive ascent (no visible flipper beats) for the final few meters to the surface (Fig. 4). On ascent, the amplitude of flipper beats was lower than on descent and was rather invariant (Fig. 5).

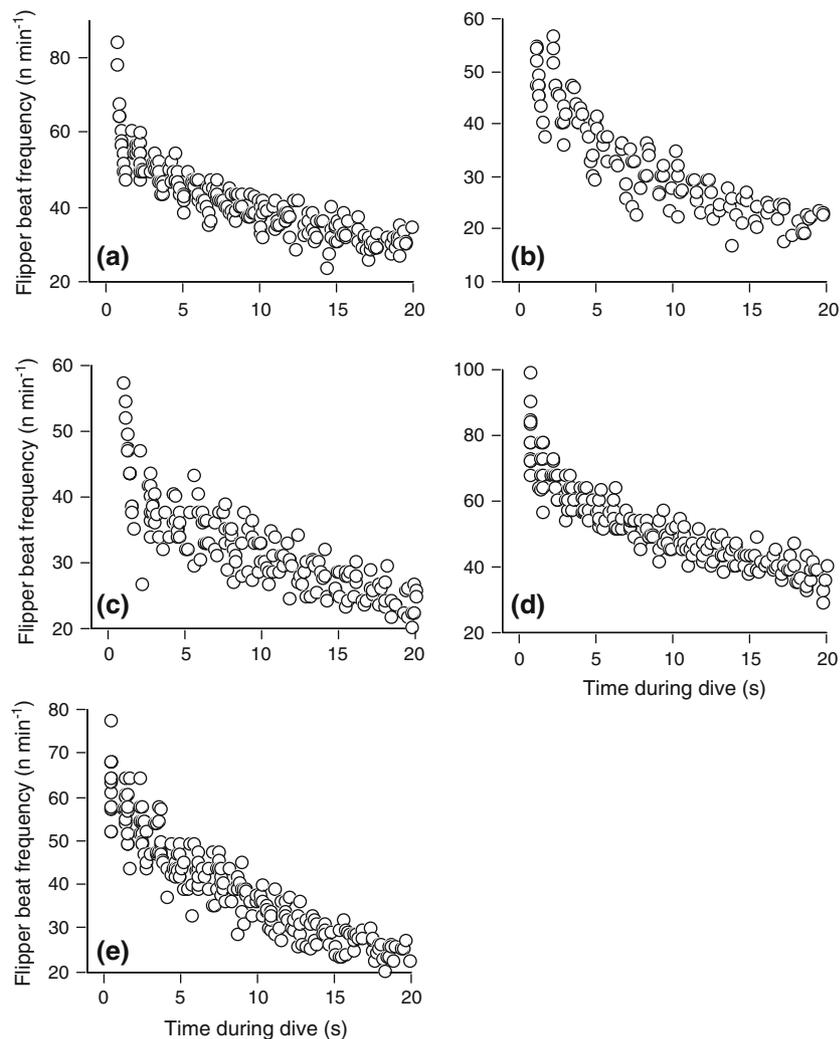
Discussion

We showed a consistent pattern of flipper beating within turtle dives, with clear reductions in beat frequency and amplitude on all descents, while ascent started with active swimming and then switched more to passive gliding as turtles neared the surface. These results help to give a clearer picture of sea turtle diving, enhancing those results obtained with time-depth recorders (TDRs). TDRs have been widely deployed on a range of species and have produced a wealth of information on patterns of depth utilization, surfacing behaviour, dive durations and depths (e.g., Southwood et al. 2005; Wallace et al. 2005). In some cases TDRs

have been interfaced with satellite transmitters to allow remote data acquisition (e.g., Hochscheid et al. 2005). However, TDRs alone do not reveal the pattern of flipper beating on dives, which may be fundamental to the optimisation of diving (Williams et al. 2000). For marine mammals and birds, the patterns of flipper beating during dives have been recorded using accelerometers, movement detecting IMASEN data loggers and cameras (Williams et al. 2000; Wilson and Liebsch 2003). However, such devices have only very recently been deployed on sea turtles. There has, consequently, been very little examination of the pattern of flipper beating during turtle diving. Hays et al. (2004b) used an IMASEN data-logger to describe the detailed patterns of flipper beating for one green turtle at Ascension Island. Recently Reina et al. (2005) pioneered the use of camera systems to record the beat frequency during leatherback turtle diving. We have shown that even subtle changes in beat frequency and amplitude within dives can readily be resolved with this camera technology. Together beat frequency and amplitude reflect the effort a turtle is expending during diving, which is fundamental to dive optimisation (Williams et al. 2000).

While the Crittercam was neutrally buoyant, it was a relatively large piece of equipment and so would certainly have increased the drag experienced by the turtles, possibly resulting in increased swimming effort. However the buoyancy of the Crittercam did not vary with depth and hence the patterns of effort we recorded within dives may be a good reflection of true behaviors. Nevertheless reducing the size of packages attached to turtles would certainly be a useful methodological advance for future studies. In addition, the Crittercam only recorded data for relatively short periods (a few hours) during which time the turtles might still have been recovering from their capture or reacquainting themselves with their local environment. Hence longer records of flipper beat frequency would be informative, allowing the patterns associated with different dive types to be examined. Furthermore the

Fig. 3 *Chelonia mydas*. Decline in flipper beat frequency during first 20 s of descent, for each of turtles 1–5 (a–e, respectively). Number of dives examined was 18, 13, 18, 11 and 18 for turtles 1–5, respectively. Linear or curvilinear regressions of beat frequency versus time during these first 20 s always showed a significant decline in beat frequency (mean r^2 for these relationships > 0.87)



causes of the individual variation in absolute flipper beat frequency warrant further investigation.

The ability of the Crittercam camera system to resolve second-by-second changes in the diving behavior of turtles clearly showed how the effort (i.e., both beat frequency and amplitude) progressively declined during descent. It is well known that as air-breathing vertebrates descend, their buoyancy declines due to compression of the gas in the lungs (and for birds air in the plumage) (Wilson et al. 1992; Williams et al. 2000). Thus the decline in swimming effort during descent paralleled changes in buoyancy, with turtles swimming with greater effort when their buoyancy was highest. This pattern was very consistent, suggesting that the patterns we recorded are a fundamental feature of the behaviour of green turtles. Similarly, decline in flipper beat frequency revealed how turtles work progressively less on ascent as their lungs expand and hence the positive lift increases. As well as the observed second-by-second changes in effort, it was also clear that

turtles worked harder (increased both flipper beat frequency and amplitude) on descent than on ascent. This finding is consistent with the expectation that the magnitude of the positive buoyancy opposing the descent is much greater than the magnitude of the negative buoyancy opposing the initial stages of ascent in both turtles and other air-breathing divers (Skrovan et al. 1999; Hochscheid et al. 2003). For example, if we assume the lung volume is 0.094 l kg^{-1} body mass (Lutz and Bentley 1985), so that a 50 kg turtle has a lung volume of 4.7 l, and that a turtle of this size attains neutral buoyancy around 15 m (see, for example, Hays et al. 2004a), then, assuming that the lungs are compressed in accord with Boyle's Law, the initial lung-induced positive buoyancy at the start of the descent would be 27.6 N. If this turtle were to descend to 25 m depth then its negative buoyancy would become only 5.3 N. Similar calculations have been performed on a range of diving species to show the same general pattern of buoyancy changes with depth (Wilson et al. 1992; Lovvorn et al.

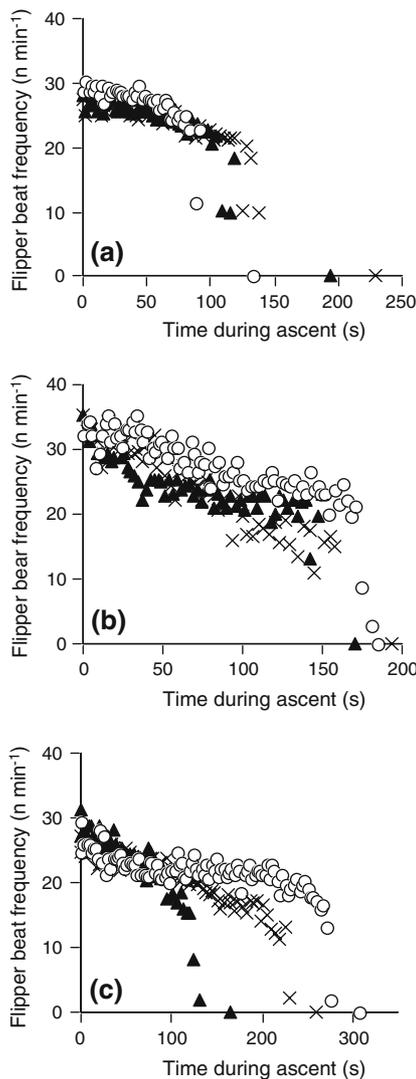


Fig. 4 *Chelonia mydas*. Decline in flipper beat frequency during entire ascent for three turtles that dived to > 30 m. Each plot shows three dives indicated by different symbols. In each case the final point indicates when the turtle broke the surface; interval between final and penultimate points indicates period of passive gliding. Panels **a**, **b** and **c** represent turtles 3, 4 and 5, respectively

1999). Where dives extend only just beyond the depth of neutral buoyancy, then the magnitude of negative buoyancy at the start of ascent will be less than that of positive buoyancy at the start of the descent.

In marine mammals and birds, where there has been far more extensive analysis of dive patterns compared to sea turtles, it has been known for a long time that aspects of dive performance, such as dive angle and descent rate, can vary in line with the function of dives and their depth (e.g., Wilson et al. 1996). Future studies with sea turtles may similarly reveal how dive performance varies with dive function and body size in this group. Our results, when viewed alongside those

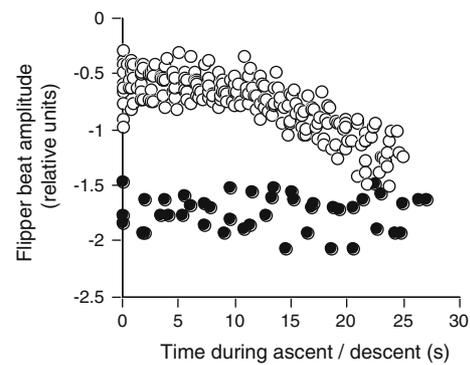


Fig. 5 *Chelonia mydas*. Changes in beat amplitude within descents and ascents for all dives by turtle 4 ($n = 11$ dives). *Open symbols* flipper beat amplitude at start of descents (first 30 s); *filled symbols* flipper beat amplitude at start of ascent (first 30 s) for 3 dives to > 30 m. Dives to > 30 m were selected as they showed the longest records on beat amplitude during ascent. For shallower dives passive gliding started within the first seconds and hence were not so suitable for showing changes in beat amplitude. Units are expressed in relation to the width of turtle's head with increasing negative values meaning smaller amplitude beats

reported for diving mammals and birds (e.g., Skrovan et al. 1999; Williams et al. 2000; Wilson et al. 2001; Sato et al. 2003), suggest that a general rule applies across a diverse range of mammalian, avian, and reptilian divers with the swimming effort paralleling changes in buoyancy, i.e., increased effort occurs when buoyancy forces oppose movement and less effort when buoyancy forces aid movement, both on ascent and descent.

Acknowledgments We would like to thank the following individuals for their field assistance: Marcos Blanco, Fernando Clemente, Steve Collins, Jennifer Gilmore, Anthony Lusk, Alexa McDermott, Antonio Resendiz, Travis Smith, and Lucy Yarnell. Special thanks go to Kira Fuchs, Scott Snider, Lynne Barre and the National Geographic Special Projects team for providing technical assistance with Crittercam throughout this project. This work was supported by Earthwatch Institute, National Geographic Special Projects, Wallace Research Foundation and the Natural Environment Research Council of the UK (NERC). Research was authorized by the Secretaría de Medio Ambiente, Recursos Naturales, y Pesca (Permit numbers 150496-213-03, 280597-213-03, 190698-213-03, 280499-213-03) and the Secretaría de Medio Ambiente y Recursos Naturales (Permit # SGPA/DGVS/002). We thank two anonymous referees for their comments which greatly improved the final manuscript.

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