Masteroppgave

NTNU
Norges teknisk-naturvitenskapelige universitet
Fakultet for naturvitenskap
Institutt for biologi

Astrid Anette Carlsen, Jonathan Wright, Svein-Håkon Lorentsen, Claus Bech, Børge Moe

Tests of the marginal value theorem in diving bouts of foraging trips in pairs of breeding European shag (*Phalacrocorax aristotelis*)

Masteroppgave i MSc Physiology and Behavioural Ecology
Veileder: Jonathan Wright
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Abstract

In this thesis adaptations of the optimal foraging model the Marginal Value Theorem (MVT) were tested using data from 46,103 foraging dives of 39 pairs of European shags (*Phalacrocorax aristotelis*) collected over 6 years, taking into account avian respiratory physiology and the effects of individual variation in body mass and the order of sequential dives. As predicted, there was evidence for a peak in the efficiency of dive durations for both sexes and for both types of dive (‘hunting’ dives with a flat bottom depth and ‘sampling’ dives without any obvious bottom duration). There were also suggestions that the birds anticipated and adjusted to the different metabolic demands of longer dives using not only air-sac O_2 but also substantial amounts of blood O_2. The shags behaved closer to the predicted optimum dive durations, calculated in terms of time efficiency, during the presumed information gathering ‘sampling’ dives with no bottom time. This suggests that the overly-long active ‘hunting’ dives involved a trade-off between the costs of less efficient dive cycles with extended surface durations versus the benefits of staying down sufficiently long to catch elusive fish prey. These results suggest that the more refined MVT model, which takes in to account the different types of avian O_2 storage (air sac versus blood) and their contrasting uptake rates, is a more accurate way of determining the time efficiency of shag foraging dives. However, important effects of individual body mass on MVT predictions were not found and clear interaction effects with dive order suggest that maintaining body temperature might also be an issue in this system. Further statistical analyses are recommended that could be used to investigate these effects in light of optimality predictions and knowledge of avian physiology.

Acknowledgement:

This thesis was written for the department of Biology at the Norwegian University of Science and Technology (NTNU), in collaboration with the Norwegian Institute of Nature Research (NINA). First and foremost, thank you to my supervisor, Jonathan Wright, for the patience during instructions, for numerous hours of good discussion and critical correction when I went astray in the labyrinth of this thesis theory, hypothesis and stats; It’s been an honour. Thank you to my co-supervisors.; Svein-Håkon Lorentsen for all the fieldwork experience, for including me in other areas of the SeaPop project and in general for all the wonderful days together at Sklinna; Børge Moe for constructive guidance in the writing process; Claus Bech for the solid foundation in diving physiology, and for many years of inspiration and encouragement within the field of physiology. Thank you Yimen Araya-Ajoy, for all the hours of helping me with the statistical analysis, for the patience and laughs while instructing me in R from the beginning till the last weeks, I am forever grateful. Thank you to all the wonderful people I’ve met through the field work at Sklinna. Thanks, all PhD candidates and other staff members at NTNU and NINA who’ve had to endure my questions, and helped me with R skripts. Many thanks to the department of physiology, the Physiology lunch group and a special thanks to Tor Jørgen Almaas for critical technical support. Thanks to my family for being the warmest, yet toughest and most hard-working of all people. Thank you to all my encouraging friends, the worlds finest. Finally, I’d like to thank the members *Sosete Physiologers Puggeklubb for Fortapte Pikebarn* (Kristin & Gina), and I can finally say with great confidence that we are no longer lost.

I denne avhandlingen ble tilpasninger av Marginal Value Theorem testet ved bruk av data fra 46.103 dykk av 39 par toppskarv (*Phalacrocorax aristotelis*) innsamlet over 6 år, med hensyn til fuglers respiratorisk fysiologi og effekten av den individuelle variasjonen i kroppsmasse samt rekkefølgen av sekvensielle dykk. Som predikert, var det tegn på et topppunkt i effektiviteten av dykketid for begge kjønn, og for begge dykketyper (‘jaktdykk’ med horisontalt bevegelsesmønster, kalt bunntid, og "informasjonsdykk» uten åpenbar bunntid). Våre funn tydet på at skarvene planla og tilpasset mengder respiratorisk- og luftsekklagret O2, i tillegg til store mengder blod og vevslagret O2. Toppskarvenes adferd var mer optimal i ‘informasjonssamledykk’, sammenlignet med jaktdykk, beregnet i tidseffektivitet. Dette antyder at de lengre aktive "jaktdykkene" innebar et kompromiss mellom kostnadene ved mindre effektive dykkesykluser (med lengre overflatetid) versus fordelene med å holde seg under vann i lang tid for å fange unnvikende byttedyr. Disse resultatene antyder at den mer raffinerte MVT-modellen, med hensyn til ulike typer aviær O2-lagring (luftsekker versus blod- og vevslager) og deres ulike opptaksrater, er en mer nøyaktig måte å bestemme tidseffektiviteten til toppskarven i dykk for matsøk. Imidlertid ble det ikke funnet viktige effekter av individuell kroppsmasse på MVT-prediksjonene, og interaksjoner med følgeeffekten av flere dykk på rad tyder på at opprettholding av kroppstemperatur også kan være et problem i dette systemet. Ytterligere statistiske analyser anbefales, som kan brukes til å undersøke disse effektene i lys av optimalitetsprediksjoner og kunnskap om fuglefysiologi.

Contents

Introduction

Being a parent bird often demands a high level of offspring care, and for seabirds this can mean traveling long distances to foraging areas, and diving for food under extreme forces of temperature, without the possibility to replenish O_2 stores (Ydenberg 2007). Provisioning young in the nest involves trade-offs in energy and time, the quantity versus nutritional quality of prey, foraging rewards versus the chance of nest being predated, as well as seasonal and circadian foraging opportunities (Wright *et al.* 1998; Ydenberg 2007). During chick rearing, hours are spent foraging every day, with ever increasing demands from the growing chicks (Ydenberg 1994). The foraging patterns of the parental birds revolve around a central place, the nest site or breeding colony, as central place foraging describes: a situation where foraging trips start and end at the same point, and foraging occurs in discrete patches within different distances from the base (Ydenberg 1994, 2007).

Seabirds that prey on fish will often seek site with certain properties indicating the presence of preferred prey, such as kelp forests or archipelagos, shoresides and shore slopes (Christensen-Dalsgaard *et al.* 2017). Parent birds have to choose between foraging patches and the time spent in them by trading off known properties such as prey availability versus flight distances from the nest. Such decision-making is best described by The Marginal Value Theorem (MVT, Charnov 1976), an optimal foraging theory that predicts how much time or effort animals should invest in each fitness enhancing opportunity to maximize efficiency (Fig.1). A parent bird is expected to maximize food delivery per time unit by bringing home larger food loads from more distant patches involving longer travel times compared to patches with short travel times (Orian & Pearson 1979). The idea is that in any foraging situation food availability will follow a diminishing returns curve (Fig.1), either due to individual exhaustion from the hunt, the limited amount of food available, limitations in means of storage room during trip (i.e. in the bill or stomach), or other physiological and ecological features (Grémillet 1996). Studies on passerine birds show that parent birds consistently adjust the load size delivered as a function of round-trip time (i.e. the distance from the nest to the foraging patch, Fig.1), as well as making adjustments concerning prey quality versus quantity and the variances in prey rewards at different locations (see Wright *et al.* 1998; Mathot *et al.* 2017; Westneat *et al.* 2017). Parent birds of most species perform self-feeding before searching for chick provisioning food (Ydenberg 1994; Ydenberg &

Davies 2010). Some choose different types or sizes of prey in different patches for them self before from prey collected for offspring (Ydenberg 1994; Ydenberg & Davies 2010).

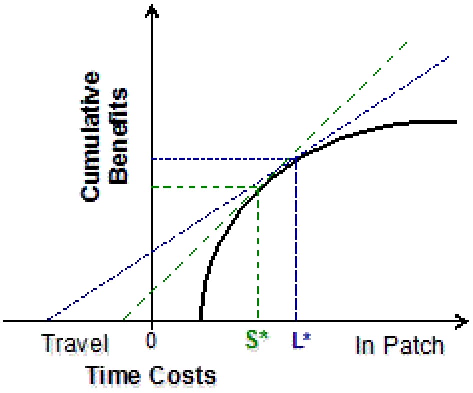


Fig.1: Graphical representation of the marginal value theorem (MVT). Arrival in the patch (at time=0) is followed by a short delay before active foraging starts with an initial rapid increase in cumulative foraging benefits (thick black curve). Benefits per time in patch then decrease with diminishing returns due to processes such as prey depletion. The optimum times in the patch for short (S* in green) versus long (L* in blue) travel times is given by maximizing the slope of the tangent to the gain curve representing the benefits per total time (travel + in patch) costs. As travel time costs increase (to the left of y-axis), then there is an increase in the optimum time spent in patch and the cumulative benefits gained per visit.

In passerines that load food up in their bills, the trade-off between self-feeding versus chick-feeding is much easier to study (Markman *et al.* 2002, 2004), as compared to seabirds that consume both types of food during the provisioning trip and then regurgitate a proportion of it for the chicks upon their return to the nest. However, even in these cases we might expect self-feeding to occur earlier in the provisioning trip (along with some digestion) followed mostly by foraging for the prey regurgitated for the chicks towards the end of the trip (Ydenberg & Davies 2010). Prey caught early in a trip may be expected to be larger, as it would mean more energy gain per prey, which should be digested quite well during the trip.

The marine system can also be quite unpredictable for a diving forager from both a short- and a long-term perspective, due to large year-to-year variations and stochasticity in prey abundance and location, as well as weather effects (Schreiber & Schreiber 1989). Marine birds are particularly adapted to such stochasticity, where one of the major areas of adjustment for survival is compromising brood investment in terms of provisioning effort (Schreiber and Schreiber 1989). The foraging pattern of many diving seabirds can be hierarchically divided into different levels: the chick rearing period last *months*, each *day* involves one to multiple foraging trips, one *trip* can include multiple locations, one *location* involves several diving bouts and inter-bout resting periods, and finally each *bout* involves a sequence of *dives* divided by *restitution periods* (combined these constitute a *dive cycle*).

Each of these dives last for seconds to minutes at a time. Flighted divers are thought to utilise switch metabolism during foraging dives (Houston & Carbone 1994), meaning that respiratory (i.e. air sac) O_2 stores are predominantly depleted first, and only once these stores are starting to become smaller will depletion of O_2 stores in blood and muscle tissue (i.e. crossing the ADL or aerobic dive limit) be utilized for metabolism (Houston and Carbone 1995). The alternative metabolic pathway in a dive is mixed metabolism, where aerobic and anaerobic metabolism is utilized simultaneously from an early stage, as a consequence of initiating induced dive response (the onset of bradycardia and peripheral vasoconstriction as a response to submersion that decreases metabolic demands, often accompanied by decreased peripheral body temperature). There are several challenges in assuming a strict metabolic pathway in dives that vary this much in duration. Flighted birds are in general not thought to utilize a strong dive response (Butler and Woakes 1979), but they have the ability of doing so if necessary (Scholander 1940) and as Houston and Carbone (1995) noted: mixed metabolism is more realistic in most cases. Further, there is a large variation in dive response initiation between closely related species (Bevan *et al.* 1997; Enstipp *et al.* 2001) within the same duration of dives. Further, the intrinsic metabolic rate of an individual is largely based on the body mass, body composition and the amount of work that is done, such as diving hunts for prey (which is thought to be a very costly affair, especially for foot propelled seabirds, see Enstipp *et al.* 2005).

During restitution periods and/or inter-bout resting periods, CO_2 needs to be dumped (Ydenberg 2007) in order to regain homeostasis in pH and partial pressures of gases in blood and muscles (Randall 2014). Even when predominantly utilizing respiratory O_2 stores, lactate might have somewhat accumulated in the tissues during local O_2 fatigue and must be transformed to CO_2 and expelled (Horning *et al.* 2012), whilst O_2 needs to be loaded up ready for the next dive(s). Refilling O_2-stores in haemoglobin and myoglobin takes considerably longer time than restoring lung and air sac deposits (Walton *et al.* 1998), and likewise getting rid of lactate is a far more time consuming and costly process than simply expelling CO_2 (Randall 2014). During the surface periods, the rate at which O_2 is loaded and CO_2 is unloaded depends on the partial pressure between the tissues and the atmosphere, a process predicted to follow diminishing returns (Houston & Carbone 1995). When applying the marginal value theorem to seabird dives during foraging, each dive is assumed to show diminishing returns (Ydenberg 2007), where the exhaustion of oxygen depots predicts the corresponding surface time (Walton *et al.* 1998).

Earlier models assumed a smooth uptake of O_2 whilst on the surface, but a more detailed model by Walton *et al.* (1998) that includes differences in uptake to the air sacs versus the blood provided more accurate predictions regarding the shape of the relationship between dive duration and the dive to surface ratio.

Diving animals can ultimately reach the end of their O_2 stores, which determines the aerobic dive limit or ADL (Kooyman 1980). When approaching the ADL, metabolism turns more anaerobic, due to depletion of O_2 stores in the associated tissues and can be seen as accumulation of blood lactate. Seabirds are often capable of enduring dives for quite a while without crossing ADL and in general avoids crossing this limit (C. Bech pers. com.). The ADL is determined by the size of the body O_2- stores and the metabolic rate during a dive (Horning, 2012), and thus larger individuals are expected to dive for longer durations before reaching the ADL. Crossing the ADL would increase the possible dive duration, but with an exponentially increasing cost (Stephens *et al.* 2007). Another way to increase dive duration is to utilize the dive response (Irving *et al.* 1935), but flying birds are not known to induce heavy dive responses in general (Butler and Woakes 1979, Hawkins *et al.* 2000) although they have the ability, for more extreme cases (Scholander 1940).

Alternatively dive duration can be increased by extensive dive preparations. In an experiment, Lasiewski and Calder (1971) found that birds were able to decrease their respiratory tract turn-over rate by half. Diving animals have the ability to prepare for longer dives by exhaling more CO_2 and stocking up on more O_2 beforehand (Collier *et al.* 1956, Lindholm & Lundgren 2009), where more time and/or effort is invested in preparing for longer dives that are more likely to provide sufficient rewards in terms of prey capture. Such pre-loading could be reflected as a longer pre-dive surface duration for longer dives, but not necessarily; The bird could increase the time efficiency by using its ability to increase its respiratory rate and thus the uptake rate of O_2 into the blood (Lasiewski and Calder 1971, Kooyman *et al.* 1973) to decrease the pre-dive surface duration in order to get back under the water while prey are still present. Loading O_2 into the additional body stores (i.e. increasing pulmonary air volume by "swallowing/ gulping" extra air into the lungs/air sacks and arterializing of venous blood) and reducing pulmonary CO_2 (through hyperventilation) during the surface period may indeed take the same amount of time as regular gas exchange, but with a much higher turnover rate

(Lasiewski and Calder 1971; Kooyman *et al.* 1973). The increased turnover rate is due to increased heart rate and breathing cycle rate, which then must have an energetic costs (Kooyman *et al.* 1973).

Although always preparing for longer than average dives could be efficient (e.g. when elusive prey might need to be pursued), it may come with a physiological cost, leading to the development of strategies that involve information gathering and thus planning the dive type prior to diving, instead. One such cost could be the stress on the cardiac muscles, due to decreased oxygenation during tachycardia accompanied by an increased O_2 demand (Elsner *et al.* 1985). Cardiac muscle can only load O_2 during the diastolic phase (between heartbeats) (Elsner *et al.* 1985), and if the diastolic phase is too short throughout surface durations when O_2 is most abundant then this may lead to lactate production in the heart (even though arterial blood is fully saturated with O_2), due to the increased work load, that could perhaps be fatal over longer bouts. The heart is well oxygenated during the decreased heart rate in dives (Elsner *et al.* 1985), but hardworking divers can have a constant compromise between exercise response (increased heart rate and blood flow) and dive response (decreased heart rate and blood flow), and so they may not decrease heart rate below resting rate and often stay quite a bit above that (Fedak *et al.* 1988, Kooyman and Ponganis 1994). If the heart muscle over tens of minutes to hour-long bouts, never get proper re-oxygenation and are often in debt during surfacing then this may perhaps be problematic, even mortal. Additionally, the pre-dive increase in heartrate and breathing rate would cost more energy (Fedak *et al.* 1988, Elsner 1985), even though it would store O_2 quicker, thus may not be worth it if it doesn't increase the chance of gain drastically. Greater mortality from the extra stress and strain on the heart may be worth it if the extra heart workload in longer hunting dives provides sufficiently more food and thus reproduction, ultimately increasing fitness.

The amount of O_2 to load, as well as time and effort to spend loading highly influence the length of the following dive. The optimum loading of oxygen can be given by the dive duration that maximized energy gain from foraging (here as time spent in horizontal movement or bottom duration), whilst minimizing the total duration costs in terms of the dive cycle (dive duration plus surface duration- see Fig. 2, Walton *et al.* 1998). Thus, a trade-off between air sac and blood O_2 stores should be evident as a bimodal dive duration; dives that are less likely to result in gained prey should end close to the peak ratio of dive duration to surface duration, while only hunting dives should require use of blood O_2 stores and thus longer surface durations and less optimal ratios.

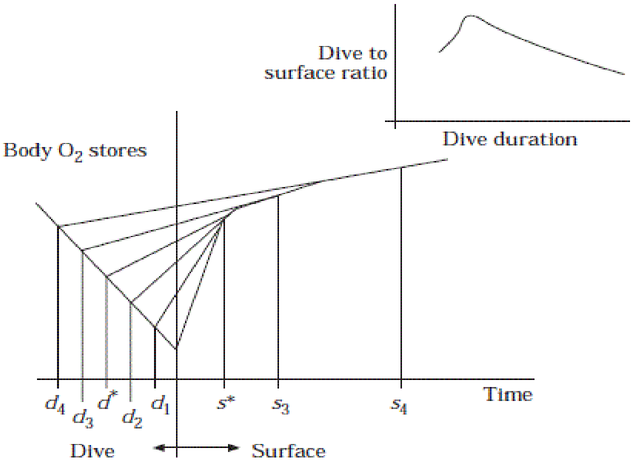


Fig.2: The relationship in the main graph between dive time (to the left of the y-axis) and time spent on the surface (to the right of the y-axis) versus the total amount of oxygen (O_2) stored in the body of a diving bird (taken from Walton *et al.* 1998). Oxygen stores decrease linearly with dive time, and increase again when they are replenished on the surface but in a non-linear fashion. The initial increase in oxygen stores at the surface is rapid as the air sacs fill with new air, but as oxygen needs to be absorbed into the blood the uptake of oxygen stores slow to a more shallow series of lines. The optimal solution that maximizes the dive time to surface time ratio is shown as s* (optimal surface time) and d* (optimal dive duration), with a range of dive times d_1 to d_4 requiring surface times for s* and s_3 to s_4 respectively. The smaller upper graph show the non-linear peaked relationship between dive time and dive to surface ratio found in various seabird species, which peaks at relatively short dives when only air sac oxygen is replenished (Walton *et al.* 1998, Cook *et al.* 2007).

The European shag (*Phalacrocorax aristotelis*) is a monogamous seabird with a single brood per season of usually 2-3 chicks, sometimes with large age or size differences between chicks within the nest (Wanless & Harris, 1997). Pairs usually divide the day into four, taking shifts of foraging versus staying at the nest (Wanless & Harris, 1997), feeding on a multitude of prey species including saithe (*Pollachius Virens*), cod (*Gadus morhua*) and sandeel (*Ammodytidae*) while rearing chicks (Wanless & Harris 1997, Hillersøy & Lorentsen, 2012). Normally each parent makes two foraging trips per day often to the same foraging location far from the breeding colony (Christensen-Dalsgaard *et al.* 2017). Male European shags are about 15% larger in body mass than females, and also show differences in body shape as well as beak and head shape (Christensen-Dalsgaard *et al.*, 2017). These sex differences in body mass may contribute to explaining why males dive about 50% deeper than the females (Christensen-Dalsgaard *et al.*, 2017), allowing the sexes to potentially exploit different foraging patches, even at the same location.

The diving strategy of a bird may be affected by its sex, body mass or a combination of the two, which should be evident by examining the effect of body mass within each sex. Larger individuals may travel to greater depths in general, and dive for longer durations per dive than the smaller individuals, and the sex difference could be a reflection of this; or there could be unrelated sex specific differences in foraging strategy. If body mass in the main determinant of depth and duration, a MVT prediction would be that longer travel distances (made easier for lager individuals) will involve fewer foraging trips (i.e. fewer, longer dives per bout) than shorter foraging travel distances (i.e. many, shorter dives per bout) by smaller individuals (Charnov, 1976). A comparison between the effects of sex (females: many, shorter dives, males: fewer, longer dives) as well as the effects modelled within each sex separately could then present a neat MVT study system.

Body mass may further change how MVT predictions are affected by the shape of the diminishing returns, given that the birds experience certain physiological or environmentally based constraints (e.g. O_2-uptake and stores, buoyancy, hydrodynamic drag, and density of prey). The allometric differences within and between the sexes are expected to have an impact on their physiological capabilities, including O_2-storing capacity and on the restoring rates, heat loss during dives, buoyancy due to body mass and composition, muscle mass and overall metabolic rates (Enstipp *et al.* 2005). Other morphological traits, such as beak size and shape may also influence the choice of prey and preferred hunting depth (Cook *et al.* 2008). Further, other effects such as seasonal changes (e.g. prey size and horizontal/vertical movement) may affect the chosen foraging strategy of the birds, especially during provisioning periods of intense foraging (Markman *et al.* 2002).

Objectives

The aim of this study was to apply the MVT to the central place foraging behaviour (Fig.1) and/or the dive behaviour (Fig.2) of the European shags rearing chicks at Sklinna, Nord Trøndelag, and to test whether individual variation and sex differences in body mass also influence these foraging behaviours. This was done by using a dataset collected at Sklinna, by the Seapop project of Svein-Håkon Lorentsen, and included GPS and TDR data (see *Methods* further down).

Hypotheses and predictions:

H^o1: Dive depth and dive duration should be positively related

Longer and deeper foraging dives should result in longer times spent at foraging depth. The MVT (Fig.1, above) predicts a positive relationship between distance to foraging location and time spent actively foraging (i.e. load size delivered to the chicks). The application of the MVT outlined in Fig.2 (above) simplistically predicts a linear covariance between dive time and maximum depth during a dive (Walton *et al.* 1998). Confirming the depth-duration relationship and other major effects on dive behaviour was an important first step in order to apply a more detailed version of the MVT to each dive that included estimates of travel times to and from the foraging depth (see Fig.3 below). A positive relationship between dive depth and duration should more suitably be captured in the travel duration within each dive. The MVT could be fitted to dives, where only time spent actively foraging (bottom duration) mattered, because only cumulative foraging duration will accurately reflect loads sizes collected per trip (assuming a constant proportion of self-feeding by the parents). This relationship was predicted to be largely independent of brood demand in seabird systems with little nutritional differences in prey types (see Wright *et al.* 1998). However, parental body mass and sex might modify the shape of this relationship.

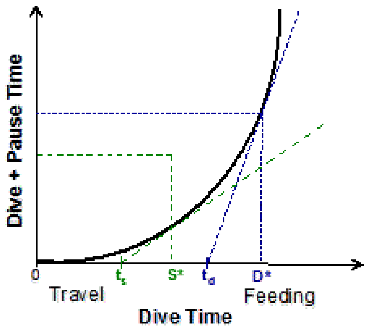


Fig.3: The relationship between dive time (composed of round-trip travel time to and from the feeding depth [time=0 to t], plus time spent feeding) versus the total amount of time required for a dive plus subsequent recovery (pause time). The relationship (thick black curve) accelerates because increasingly lengthy pauses are required to recover after longer dives. The marginal value theorem (MVT) again shows the optimal solution for shallow dives (S* in green) versus deep dives (D* in blue) by minimizing the slope of the tangent to the cost curve. As dive depth increases (t_s to t_d), then there is an increase in the optimum total required dive time plus pause time. Adapted from Box 1.2 by C.W. Clarke in Stephens *et al.* (2007).

We predict that any further relationship between dive depth and dive duration is explained by random effects such as the large energy amount required by thermoregulation, influenced by the loss of body heat in colder waters at larger depths, as well as the energy requirement of foot propulsion (Enstipp *et al.* 2005). Foraging periods at greater depths should therefore require relatively quicker returns to the surface (i.e. shorter foraging durations) than expected for more shallow dives.

H^o2: The dive duration to surface duration ratio should peak at intermediate depths

As outlined above in Fig.2, this peak in dive to surface duration ratio determined by the oxygen stored in air sacs versus in the blood haemoglobin and myoglobin. We therefore predicted a later peak for larger (i.e. male) birds with presumably larger air-sac capacities. By subtracting the observed travel duration from the optimal dive duration, the predicted bottom duration can be determined. The optimality in foraging behaviour can then be established (Fig. 3) by finding the correlation between predicted and observed bottom duration. The proportion of the dive time spent travelling versus foraging (Fig.3) was predicted to have no effect, unless they involved different energetic demands and therefore different oxygen depletion rates. Active foraging was recognized as the part of a dive with distinct horizontal movement.

Another prediction here was that if no prey was detected early on in a dive during the use of oxygen from the air sacs, then birds might prematurely end such ‘sampling’ dives at the optimum (peak) efficiency upon depletion of oxygen stored in air sacs. Dives when prey was detected and pursued were predicted to last beyond this point, perhaps exhausting oxygen stores in the blood as well. This predicted bimodal distribution of dive durations was expected to result in a bimodal distribution of surface durations after (rather than before) the dive in question. Again, we predicted additional effects of sex and body mass.

H^o3: There should be a dive order effect within and between dive bouts

To investigate if birds got fatigued due to build-up of lactates or due to reduced body temperatures, we predicted that later dives within a dive bout would be shorter and involve greater subsequent surface time, depending upon cumulative dive times. The path of effects on the surface duration after a dive may even be affected by how much time the bird spent on the surface before the dive, or the amount of preparation the bird underwent before the dive. Longer dive bouts were predicted to be followed by longer inter-bout intervals, which were used to allow birds to recover. Again, we predicted additional effects of body mass and/or sex of the bird, where small individuals showed shorter dive bouts and shorter inter-bout intervals than larger individuals.

Materials and methods

Study Site:

The Sklinna archipelago, situated about 20km off the coast of Vikna in Trøndelag (65°12'N 10°59'E), has been a dedicated Ramsar site since 2010 (Ramsar 2012). Sklinna holds one of the largest shag colonies in Norway (Hillersøy and Lorentsen 2012), with ca. 2,000 breeding pairs in 2017 (S.-H. Lorentsen pers. comm.), as well as breeding colonies of common guillemot (*Uria aalge*), black guillemot (*Cepphus grylle*) and Atlantic puffin (*Fratercula arctica*) (Ramsar 2012). The SEAPOP (www.seapop.no) project was initiated as a long-term monitoring program for seabirds along the Norwegian coast, Svalbard and the associated marine areas. The program has resulted in an increased understanding of Norwegian seabird populations, and has largely contributed to the way the populations are managed.

Data collection:

The fieldwork for this specific study was conducted in June-July 2013-2018. The shags were sexed by sound when approached, and captured off their nest using snares. Afterwards each individual was fitted with GPS-loggers (in 2011 Earth and Ocean mGPS-2, otherwise i-gotU GT-120, Mobile Action Technology, re-fitted in heat shrink tubes) and Time Depth Recorders (G5, CEFAS Technology). TDR-loggers were attached to the GPS-logger prior to instrumentation using TESA® tape. The GPS-loggers were attached to 3-4 middle tail feathers using strips of TESA® tape. The maximum weight of the deployment when using both GPS- and TDR loggers was 30.6 g, corresponding to 1.6% and 1.8% of mean body mass of males and females at Sklinna, respectively. The GPS-loggers recorded location (± 10m) every 30 sec, and the TDR recorded water depth below (± 0.1m) every second. The loggers were removed after approximately 2-5 days, using scissors to cut the tape, with rare damage to the feathers.

Deployment of loggers normally required less than 3 min of handling and retrieval less than 10 min. Birds were fitted with loggers during the chick-rearing period (June-July) starting in the late phase of incubation until chicks were approximately 35 days old. Chick age was determined using morphological criteria determined from control nests (another study within the Sklinna colony) checked every fifth day. Sex of the adults was determined by size and vocalization (cf. Cramp and Simmons 1977). At capture the body mass of the adult and their chicks were obtained using Pesola spring balances (accuracy 0-100g ± 1g, 100-500g ± 5g, > 500g ± 10g). At recapture biometric measures of the adult wing-length (ruler ± 1mm), head + bill length (digital caliper ± 1mm) and body mass (see above) and the chick head + bill length and tarsus length (digital caliper ± 1mm) and body mass (see above) were obtained. Female average mass was 1610g (min: 1370g, max: 1860g,), whilst average male mass was larger at 1920g (min: 1660g, max: 2280g, [620g]), a total span of 910g within observations.

Sample size was 78 birds (39 pairs) over 6 years. Shags were semi-randomly chosen from the more 'protective' pairs of adults (i.e. those that stayed around the nest and were therefore easier to capture), based on the age of the offspring in the nest (see above) and aggression when approached, because of the increased chance of subsequently recapturing such protective adults. Each individual was recorded over 2-4 days, both individuals in the pair were recorded in the same period, though not overlapping in time, usually with only a few days between. Nests were also chosen for easy accessibility. A total 24 locations were qualitatively estimated from squared areas where dives occurred, based on similar average depth determined from a topographical base map by Kystverket (https://kart.kystverket.no/). The GPS-location was abbreviated to 2 decimals (See Appendix S1). The size of locations and number of observation varied between locations.

Data handling:

The TDR raw data, collected by the SeaPop project over 6 years, were run through R library DiveMove (Luque, 2007). A minority of extremely large dive durations values were not removed from the data as there were no obvious criteria to suggest that these were data errors, and the large number of observations here should minimise the effects of any such extreme values. The total number of dives in this study was 46,103. The surface for dives was calibrated at +/-1m, so that no dive movement less than 1m depth was counted as a real dive. Further, bottom movement was calibrated with the DiveMove zoc method (Luque, 2007), smoothed using depth filters, for depths between 4 and -4m. The time submerged was divided into mainly vertical versus mainly horizontal movement, with respect to direction and movement within the smoothed depth. Movement downwards was registered as descent, horizontal movement within the ±4m smoothing filter was registered as bottom duration, and the dives were started/ended by crossing the 1m threshold of smoothed surface.

GPS locations for dives were chosen from the closest measured in time to a dive, within 30s before/after, due to GPS location not recorded during dives. GPS data handled by R library ggmap (Kahle and Wickham, 2013). Merging, combining and tidying etc. of data set was preformed using dplyr (Wickham *et al.*, 2018), and plots were generated by ggplot (Wickham, 2016).

Data analysis

All data analyses were performed in the R version 3.5.1 (2018). Description of main parameters can be found Table 1. The data was ordered; first by identity, and then by time of dive within identity. The main method for data analysis was mixed effect models, conducted with R library lme4 (Bates *et al.* 2015). In Section 1 of the Results, models were fitted to all main parameters (maximum depth, dive duration, travel duration, ascending duration, descending duration, bottom duration, pre-dive duration, post-dive duration, bout length, dive cycles and ratios – see Table 1 for a glossary of the main parameters), with different predictors as fixed effects (sex, dive type, sex, body mass and dive order within a bout), while controlling for random effects within and between grouping in the data (identity, location, year and dive date). Note that by including individual identity (ID) variation as a random effect in mixed models, any additional variation caused by the individual differences in body masses was controlled for, even if the fixed effect of body mas was not included in the model. Similarly, any seasonal changes will also have been controlled for in the random effect of dive date even without an explicit fixed effect of dive day being added to models. Body mass and dive day were therefore sometimes also included as fixed effects to investigate their direct effect on the mean of the response variables, but otherwise these effects were controlled for in the random error structure of these models.

Pre- and post-dive durations longer than 360s were used to separate surface durations too long to be explained by replenishment of O2 storages or resting within a bout, and were assumed to represent travel between locations prior to the start of a new foraging bout, termination of foraging trips or social behaviour. Residual distributions were tested for normal distribution (for confirmation, see Appendix Fig S1), with Poisson distributions being used for variables involving counts. A slight residual skew was found in models for surface duration (See Appendix S1), but neither fitting generalized linear models handling Poisson distribution nor log-transformation provided effective solutions, and so no further action was taken. Estimated effect sizes are given with 95% confidence intervals (CI) and random effects were calculated as proportions of total variation explained. AIC values were used to find the best-fit models to decide upon the inclusion/exclusion of interaction terms or second order polynomial relationships (e.g. body mass squared or dive order squared) – see Forstmeier & Schielzeth (2011). Curvilinear (i.e. second-order polynomial) effects were removed from models whenever non-significant or un-recommended by an increased AIC score, along with any linear effects as well when justified by these protocols of model reduction. Residuals distribution was checked with residual histograms, and normality of data tested with qqplot (Becker *et al.* 1988).

In Section 1 of the Results, models involving bout length and dive order as response variable were fitted with GLMER (generalized mixed effect models). Dive order was mean centered due to bouts length variation within sexes and individuals, and to investigate difference in relative order effects within bouts. In sub-section 1B, the curvilinear second-order polynomial effect of dive order and mass, although significant (see Appendix, Table S3, Fig. S3, and Table S4, Fig. S4) had an effect size less than 5%, and usually less than 1% of the linear component effect. It was thus removed from Table 4 models to simplify these analyses, and to avoid multiple 2-way interactions between all of the linear and curvilinear terms. The linear and second-order polynomial effect of dive order and body mass separately can be found in the Appendix (Table S3 and Table S4, respectively). In Table S4, the differences in sex and body mass effects were determined by running simple linear models for both dive types. Sex difference was based on models with only sex as a fixed effect for all main parameters; Body mass effect was calculated from effects by models with the body mass effect for females only (without separation for dive type), and multiplied with the mean weight difference between females and males (see Data Collection above).

All analysis in Section 2 of the Results were based on a slightly reduced data set where all dives with a NA recorded surface duration (e.g. first and last dives in a bout) were removed to avoid erroneous infinite values being calculated for dive cycles and dive ratios, ending with a total of 42.014 observations. In Section 2A.1, exponential models were selected in accordance with MVT prediction (see Fig.3) through the coefficient of determination (R^2) by MuMIN package (Barton, 2018). In all cases, R^2 was 2-15% higher for exponential models than linear and polynomial curve fits. By fitting exponential curves to the dive cycles, the observed travel durations were subtracted from the optimal dive duration (determined by the exponential model) and thus predicted bottom durations (see sub-section 2B.2) could be estimated (see Fig.3, Stephens *et al.* 2007). Further, dive cycles were log-transformed in all sub-section 2A analyses to allow linear (i.e. lognormal) versions of these exponential relationships to be assessed in the linear mixed models. The optimal dive duration and thus predicted bottom duration in the Section 2A.1 analysis was based on the raw data of the same dives, resulting in a loop within the analysis that is far from perfect. A refined analysis of the optimal behaviour was conducted by plotting the ratio of the dive duration to surface duration against the increasing dive duration (as in Walton *et al.* 1998). Predicted bottom duration (Subsection 2A.2) was found by subtracting the observed travel duration from the optimal dive duration given the exponential models (See Table S6). The correlation between predicted and observed bottom duration for WBD dives was established through Pearson's correlation test. Ultimately, the predicted bottom duration would be estimated by taking the tangent line from the diminishing returns dive cycle-curve, the x-intercept would be the corresponding travel duration, and by inverting this relationship, the tangent line from each observed travel duration would correspond to a point at the curve, which x-coordinate would be the optimal dive duration for that given travel duration. By subtracting the observed travel duration from the optimal dive duration, the predicted bottom duration would be determined. However, there was issues with making optimal values correspond to each of the observed values especially as we observed values that simply 'missed' the optimal curve, due to practically being too long for the curve estimate. Further, the optimal dive duration would never be estimated to be lower than 33s, due to the nature of the tangent crossing the y axis at positive values of y. This means that it would not have been able to predict a bottom duration in shorter dives although avoiding the issue of negative predicted bottom durations. Thus, as an alternative we decided optimal dive duration from the diminishing returns dive cycle curve, and subtracting observed travel duration from this. The other approach should however be revisited at a later time.

Piecewise (i.e. 'broken-stick') linear regressions were fitted to bottom duration (Section 2B) and dive cycle ratios (Section 2C.1), using the R-package Segmented (Muggeo, 2008). Linear regression lines were run for each possible break point (point of change in directions for the observations), using log likelihood. Best estimate was chosen as prediction for modeling break point. Data was tested for several slopes, and models were tested with AIC. Models were fitted with a smoothing algorithm. The piecewise linear regression had a tendency to skew break points, partly due to the grouping of data into 5s intervals, as well as due to the lack of correction for groupings in data, as the segmented linear regression didn't allow random effects. The uncorrected pseudo-replication was also evident in intervals including very variating number of observations (ranging from 2 datapoints to over 2500). Note that pseudo-replication may have affected the positioning of the dive to surface peak ratio, as the piecewise linear regression could not take the groupings of data into consideration, not taking nesting into account and thus, overrepresenting individuals with most recorded dive observations. Median dive durations given in section 2C.1 (Fig. 13 and Fig. 14, and Table 7a) were retrieved from a data set where dives without either pre- or post- dive duration excluded (i.e. reduced dataset -see above). Finally, a path analysis was used to explain how one part of a sequence of events directly and/or indirectly affects other parts. In the path analysis presented in sub-section 2D, response variables were log-transformed in the mixed models for a more standardized result interpretation, and better fit of model to data as well as normality of residual.

Table 1: Description of the parameters derived mainly from GPS, TRD and demographical data used in the study.

Parameter	**Description**
Maximum depth	The deepest vertical distance from surface in meters per dive.
Dive duration	Total time spent underwater in a dive, including *descent duration, bottom duration* and *ascent direction*.
Descending duration	Time spent in vertical movement descending
Bottom duration	Time spent in horizontal movement per dive.
Ascending duration	Time spent in vertical movement ascending
Travel duration	Total of *descent duration* plus *ascent duration* within each dive.
Pre-dive duration	Time period spent on the surface before each dive, with surface durations >360 secs excluded – see definition for *bout length* below.
Post-dive duration	Time spent on the surface after each dive, with surface durations >360 secs excluded – see definition for *bout length* below.
Dive order	The consecutive number of each dive within a *bout*, which was mean centred for all analysis to control for individual and sex differences in *bout length*.
Bout	A sequence of dives within individual, defined by *Pre-* and *post-dive durations* <360s (See methods).
Bout length	The number of consecutive dives, treated as Poisson distributed data.
Dive type	Dives with and without bottom duration (*No Bottom Duration (NBD) dives and With Bottom Duration (WBD) dives)*.
No Bottom Duration (NBD) dives	Dives with no *bottom duration*, assumed to be sampling dives involving no active foraging. Binomial value 0.
With bottom duration (WBD) dives	Dives that included *bottom duration*. Binomial value 1.
Dive cycle before (DCB)	The *dive duration* plus *pre-dive duration* per dive.
Dive cycle after (DCA)	The *dive duration* plus *post-dive duration* per dive.
Dive ratios before (DCBr)	The ratio between *pre-dive duration* and *dive cycle before* per dive, excluding any dives with *pre-dive durations* of zero.
Dive ratios after (DCAr)	The ratio between *post-dive duration* and *dive cycle after* per dive, excluding any dives with *post-dive durations* of zero.
Year	Including the 6 years from 2013-2018.
Individual (ID)	Identity by ring number.
Day	Dive date, a continuous measure of days from the earliest to the latest day of the season, based on date regardless of year. From June 22. to July 16. (range 25d).
Location	24 locations determined from a topographical base map by Kystverket, with respect to mean depth (https://kart.kystverket.no/).

Results

Section 1:

Section 1A.1: Sex and dive type

The effects of sex and dive type, as well as their possible interaction, were estimated on each of the main dive parameters separately (Table 2, Fig. 4a-f). The main intention here was to see at the start of the analyses if the two sexes, and the presumed two dive types, did in fact represent different groups or sub-sets of the data.

There was a strong effect of dive type - no bottom duration (NBD) versus with bottom duration (WBD) dives - on all of the dive parameters, although not surface durations (Table 2). This strongly suggests that the distinction into the two types of dives is valid, perhaps equating to sampling dives where no prey was caught (NBD) versus hunting dives where prey was actively pursued and perhaps caught (WBD) – see Discussion. There was also a strong effect of sex (male versus female) on all dive parameters, including surface durations (Table 2). This might reflect sex differences in body mass, but the two were hard to separate statistically (see below). There were also significant interactions between dive type and sex, which complicates any interpretation of these different effects. For these reasons, all subsequent analyses were carried out separately for each sex and dive type.

Table 2: Results of mixed models for the different dive parameters showing the fixed effects of two different dive types (no bottom duration versus with bottom duration), sex differences (male versus female) and their interaction, with effect sizes (for non-standardized values) and 95% CIs. Individual identity, location, year and dive date were fitted as random effects, which are given as proportions of total variation explained. Bold numbers for significant values, except in intercepts.

	Max depth (m)	Dive duration (s)	Descending duration (s)	Ascending duration (s)	Pre-dive duration (s)	Post-dive duration (s)	Bout length (s)
Intercept Males NBD	17.47 (14.30, 20. 89)	44.44 (37.82, 51.07)	24.12 (20.71, 27.43)	20.49 (17.98, 22.82)	54.45 (42.92, 66.05)	53.59 (42.38, 65.48)	2.63 (1.92, 3.43)
Females NBD	**-4.87 (-6.74, -2.85)**	**-10.08 (-14,05, -6.24)**	**-5.79 (-7.66, -3.74)**	**-4.82 (-6.18, -3.46)**	**-13.33 (-20.55, -6.59)**	**-13.26 (-19.45, -6.66)**	**0.56 (0.27, 0.84)**
WBD	**2.24 (1.89, 2.61)**	**12.20 (11.34, 13.10)**	**-1.66 (-2.29, -1.14)**	**-3.86 (-4.24, -3.46)**	-1.20 (-3.31, 1.05)	0.92 (-1.11, 2.92)	**0.48 (0.41, 0.54)**
Sex-Dive type interaction (Female WBD)	-0.0002 (-0.21, 0.21)	**-0.71 (-1.24, -0.19)**	**1.33 (1.02, 1.64)**	**1.81 (1.58, 2.05)**	0.29 (-1.00, 1.50)	0.37 (-0.83, 1.58)	**-0.22 (-0.26, -0.18)**
ID	0.30	0.24	0.21	0.16	0.17	0.16	0.14
Location	0.13	0.03	0.10	0.09	0.00	0.08	0.39
Year	0.00005	0.03	0.002	0.00	0.01	0.01	0.00
Dive date	0.09	0.08	0.05	0.06	0.002	0.03	0.15
Residual	0.48	0.62	0.64	0.69	0.82	0.73	0.32

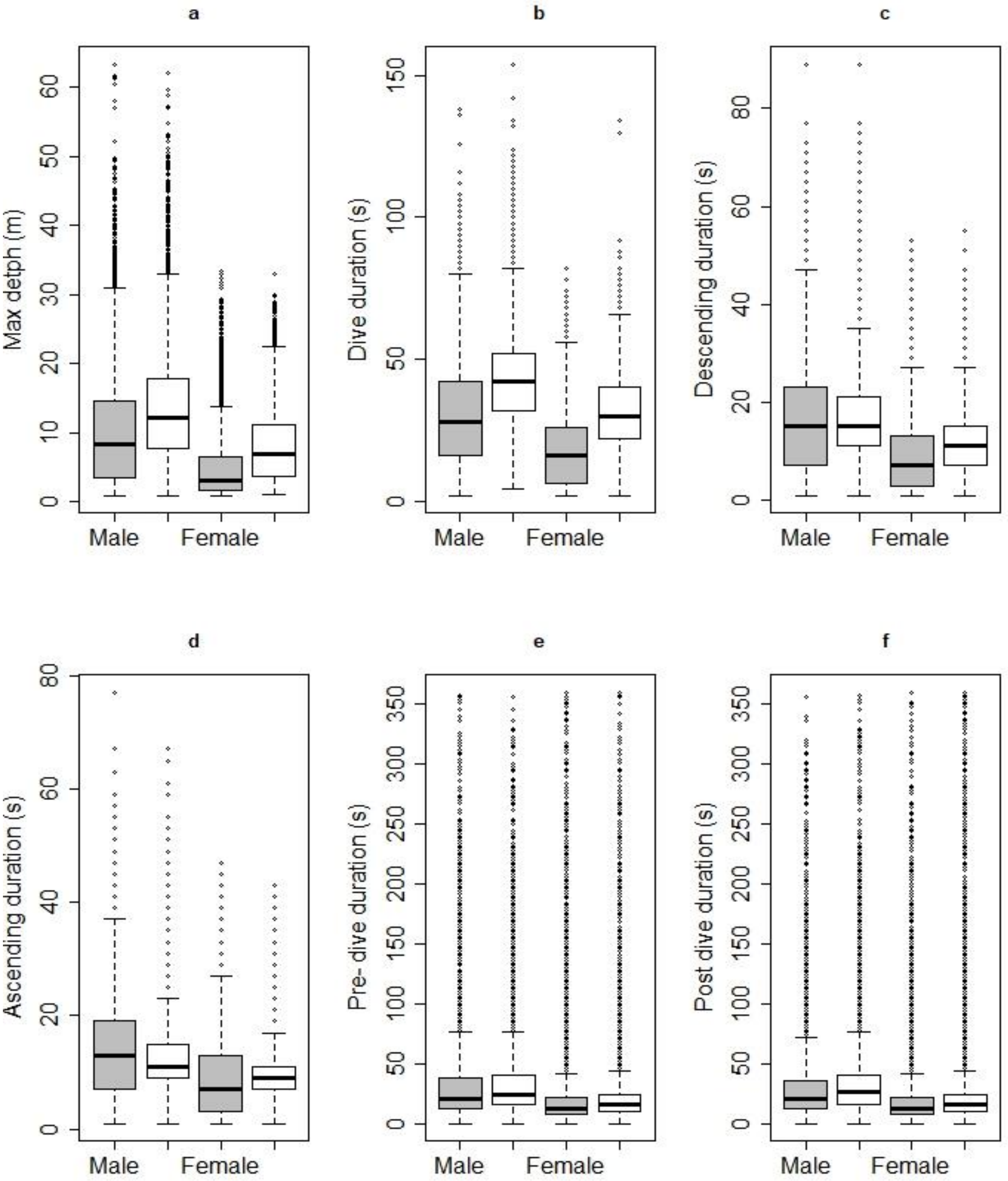


Fig 4: The effects of dive type (no bottom duration NBD [grey] versus with bottom duration WBD [white]) and sex on the different dive parameters - see Table 2. a) Maximum depth, b) Dive duration, c) Descending duration, d) Ascending duration, e) Pre-dive duration and f) Post dive duration. Based on residuals, mean values are indicated with black bars, and boxes for the interquartile values, error bars represent standard error, and outliers with all raw data included.

Some more detail is now provided here to help with the interpretation of the results in Table 2, whilst the random effect results from all these various models are discussed below (Section 1D).

Maximum depth was on average 17.47m (14.30, 20.89) for NBD dives, and increased a further 2.24m (1.89, 2.61) for WBD dives, showing that the birds dived deeper before any horizontal hunting movement started. Sex had a large impact on the preferred maximum depth, with male birds going on average 4.87m (6.74, 2.85) deeper than females, which might reflect sex difference in body mass (see below). However, there was no significant sex by dive type interaction in this case (Table 2; Fig. 4a).

Dive duration was on average 32.24s (26.48, 37.97) for female birds for NBD, and 44.44s (37.82, 51.07) for male birds. Dive duration increased by 12.20s (11.34, 13.10) for WBD (hunting) dives. Male dive durations were longer by 10.08s (14,05, 6.24), and sex and dive type showed a significant interaction, with an additional increase of 0.71s (1.24, 0.19) for females during WBD dives (Table 2; Fig.4b).

Interestingly, the results for descending versus ascending durations differed between the sexes (Table 2; Figs 4c & d). Ascending for males took on average 20.49s (17.98, 22.82), less time than descending for 24.12s (20.71, 27.43) for NBD dives, suggesting an effect of buoyancy working against descents and helping with accents (see below). The sex differences here (due largely to sex differences in maximum depth, Table 2; Fig.4a) are slightly larger when descending (female birds -5.79s (-7.66, -3.74) faster) than when ascending (female birds -4.82s (-6.18, -3.46) faster). These sex differences should perhaps be equal if it was just a matter of a sex-specific (or mass-specific – see below) differences in diving behaviour, perhaps the females move towards the surface during the bottom duration decreasing the distance of ascent, but the description of the parameters and algorithms given are not detailed enough to be sure.

Therefore, perhaps there was some non-linear changed in swim speed with depth due to the different effects of buoyancy when descending versus ascending (see Section 1C below). The interaction between sex and dive type was similar in scale in descending versus ascending durations (1.33s (1.02, 1.64) versus 1.81s (1.58, 2.05), respectively), again, possibly reflecting a non-linear difference in effect size between the sexes. The positive effect for females in WBD dives suggests a small additional effort in depth reaching made by females (maybe when prey were detected).

Pre- and post-dive surface durations showed similar results throughout, which is perhaps unsurprising as these two variables include much of the same data from the majority of dives (see Methods, Table 1). Dive type (NBD versus WBD) had little impact on surface durations, and there were no interactions with sex (Table 2; Fig. 4f & g). Females spent -13.33s (-20.55, -6.59) less time before and -13.26s (-19.45, -6.66) less time after a dive on the surface, as compared to males that on average spent 54.45s (42.92, 66.05) on the surface before a dive and 53.59 (42.38, 65.48) s after a dive. This makes sense when comparing the surface durations (Fig.4d & e) to the dive durations (Fig.4b), because male birds had significantly longer dive durations than female birds, both in NBD and WBD dives, hence they might be expected to need longer time on the surface to load or restore greater volumes of O_2.

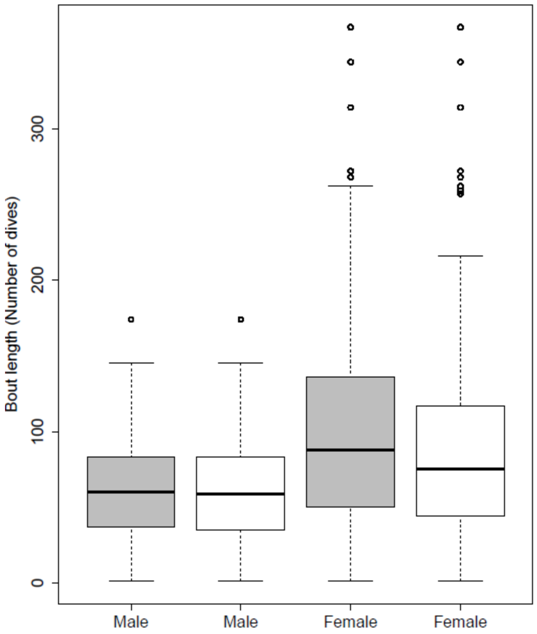


Fig 5: The effects of dive type (no bottom duration NBD [grey] versus with bottom duration WBD [white]) and sex on bout length. Based on residuals, mean values are indicated with black bars, and boxes for the interquartile values, error bars represent standard error, and outliers with all raw data included. See table 2a & b.

The mean bout length was 29.50 dives for males, and significantly longer at 41.68 for females (Median: males 59 dives per bout, females 82 dives per bout). Dive type significantly affected number of dives in a bout, and there was an interaction between sex and dive type. Longer bouts contained more NBD dives for females, but this was interestingly not the case for males. The random effect of location had a large effect on bout length, and the female strategy here may have been to use more NBD dives to search for possibly more scarce prey at lower depths or to scare prey from hiding places, such as kelp dense patches – see Discussion. As noted above, the average NBD dive depth for males was 17.47m, and 12.62m for females, perhaps reflecting sex differences in body mass, but these two effects could not be separated in this analysis.

The large difference in bout length for males and females (Fig. 5) suggests that an effect of dive order should have a different total impact on females with their longer bouts than on males with their perhaps more demanding dives (deeper, more long lasting). The effect of increasing number of dive order and bout length was explored in the next Section 1A.2 on frequency of dive types in the beginning versus the end of bout.

Section 1A.2: How dive type changes with order and bout length

Individual dive bouts were examined to estimate the linear effect of increasing number of dives in a sequence for each individual dive (dive order) and on the total length of a bout (bout length). The models were fitted with Poisson distribution (generalized mixed effect model) and the dataset separated between the sexes, but not dive type. Dive order was mean centered as the length of bouts highly differed, thus mean centered dive order returned the value for the mid dive in the order, no matter bout length, to compare difference in order effect between the first (pre-mid-dive) and second (post mid-dive) half of a bout.

WBD dives were more common at the beginning than the end of bouts for females (Table 3a), but not for males (-5.02e-3 (-3.50e-2, 7.92e-4)). Females had 55% NBD dives, whilst male had 66%, but females also had longer bout lengths (Table 1). However, longer (mean-centered) bout lengths within each individual tended to have a higher rate of NBD dives (Table 3b), especially for females (-0.85 (-0.86, -0.84)) but also for males (-0.36 (-0.38, -0.35)). This suggests that relatively longer bouts for each individual (i.e. when they had not terminated the bout early and with more WBD dives due to gathering sufficient prey) tended to end on a losing streak of NBD dives. Excessive numbers of NBD dives may thus be a sign of a decreasing rate of prey encounter, causing birds to end a bout, possibly traveling to another hunting location. Alternatively, bouts were ended not because of a lack of prey but because individual reached some physiological limit of successive dives (e.g. lower thermal threshold, lactate production, etc.) – see Discussion.

Table 3: The effect on dive order (a) and bout length (b) by dive type, separated by sex. Mixed effect models included identity, location, year and dive date as random effects, which are given as proportions of total variation explained. Fixed effects are given as effect sizes (for non-standardized values) with 95% CIs. Bold numbers indicate significance in fixed effects, except in intercept.

a) Dive Order		
	Female	Male
Intercept	2.91 (2.31, 3.54)	2.28 (1.88, 2.71)
Dive type	**-5.26e-3 (-9.00e-3, -1.74e-3)**	-5.02e-3 (-3.50e-2, 7.92e-4)
ID	0.04	0.02
Location	0.25	0.15
Year	0.01	0.00
Dive date	0.02	0.02
Bout ID	0.41	0.47
Residual	0.27	0.34
b) Bout Length		
	Female	Male
Intercept	4.62 (3.73, 5.50)	3.79 (3.47, 4.10)
Dive type	**-0.85 (-0.86, -0.84)**	**-0.36 (-0.38, -0.35)**
ID	0.04	0.10
Location	0.53	0.22
Year	0.00	0.00
Dive date	0.20	0.06
Residual	0.22	0.62

In order to better understand what the length of hunting dive durations was determined by, the distribution of dive durations for WBD dives was investigated. The distribution of dive durations in WBD dives for females and males (Fig. 6) were surprisingly close to normally distributed, suggesting that the length of a dive was not determined by some physiological limit. If there was a strict physiological limit, then the WBD dives in Fig.6a & b would be expected to have shown a right truncated Poisson distribution, revealing the threshold for the aerobic dive limit. This therefore suggests that WBD dive durations are the result of some more gradual cost-benefit trade-off, such as the diminishing returns of prey encounter in a patch, or simply the amount of time/effort it takes to catch a pursued prey or to give up on trying. The data we have does not make it possible to distinguish between such effects without capture success information per dive.

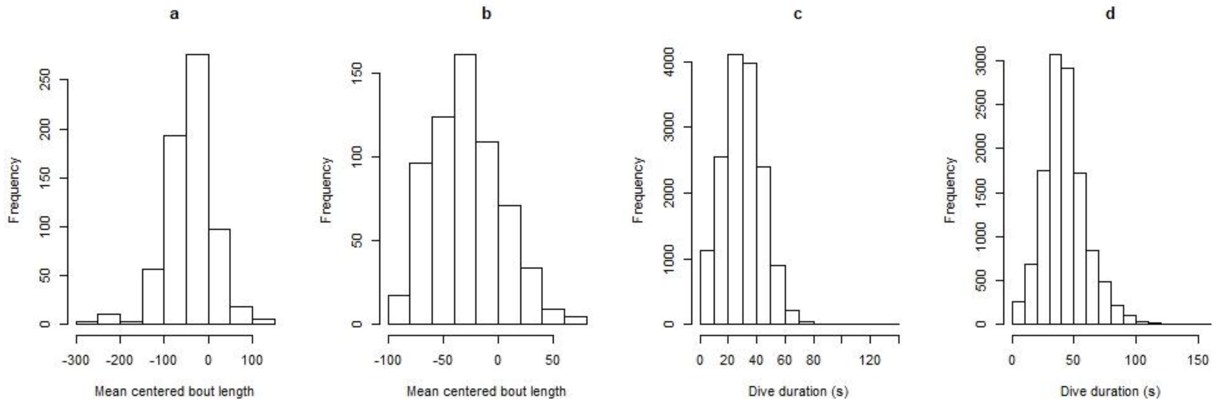


Fig 6: Distribution frequencies in WBD (with bottom duration dives) dives for a) Female dive durations and b) Male dive durations, and for c) Female bout lengths and d) Male bout lengths.

Section 1B: Body mass and dive order within bouts

The findings in Sections 1A.1 and 1A.2 suggest rather large effects of sex and dive type plus interactions between the two, and confounded effects of sex and body mass. Therefore, it was decided to split all subsequent analyses into the two types of dives (NBD and WBD) and the two sexes separately, in order to understand more clearly the nature of diving behaviour in this system. In this sub-section, we explore the effects of body mass and within-individual variation in dive order on the different dive parameters, where dive order was mean centred within bout - see methods.

During initial investigations, we detected a statistically significant curvilinear effect of the second order polynomial terms for both body mass (Table S3) and dive order (Table S4). However, the effect sizes of these were below 2% of total linear effect, and thus unlikely to be biologically significant (see appendix). Therefore, in order to simplify the analyses presented here, and especially any interactions between body mass and dive order, only the linear terms have been included in the models in Table 4.

In general, body mass had a large effect on most of the dive parameters for females during both dive types, with the exception of surface durations and bout length (Table 4a-b). Males showed no main effects of body mass on dive parameters, but there was an interaction between body mass and (individually mean-centred within bout) dive order for males in most parameters and for both dive types (Table 4a-b), complicating the interpretations here. For females, the interactions were less evident. In WBT dives, interactions were only found for females in maximum depth, and in NBT dives there was a significant interaction in dive duration, reflected in both descending time and ascending durations.

The lack of interactions between dive order and body mass in females compared to males is interesting. Both parameters returned large effects separately in females (Tables S3 and S4), but when modelled together (Table 4a-b) dive order often lost its effect once body mass was controlled for, and there was little sign of any interaction. Males on the other hand showed little effect of body mass alone, but still there was an interaction of the effect of body mass with increasing dive order. It seems likely that body mass may have had a larger effect in longer bouts (i.e. for higher dive numbers), but since males often chose to stay within the lower number of dives (see Section 1A.2), the effect was less obvious for males. Females often had 30% more dives per bout suggesting the effect of body mass was more important due to these lengthy bouts.

Table 4: The effect of body mass and (individually mean-centered) dive order within each bout on the dive parameters maximum depth and different dive durations and surface durations separated by sex for (a) no bottom duration (NBD) and (b) with bottom duration (WBD) dive types. Dive order is mean centered per individual to remove any confounding effects on the length of bouts. Mixed effect models included identity, location, year and dive date as random effects, which are given as proportions of total variation explained. Fixed effects are given as effect sizes (for non-standardized values) with 95% CIs. Bold numbers for significant values, except in intercepts.

a) Females NBD dives

	Max depth (m)	Dive duration (s)	Descending duration (s)	Ascending duration (s)	Pre-dive duration (s)	Post-dive duration (s)	Bout length (n)
Intercept	-9.26 (-20.50, 1.72)	-23.64 (-53.54, 5.33)	-9.30 (-24.94, 5.43)	-11.16 (-25.10, 3.10)	14.48 (-14.53, 43.46)	20.45 (-4.70, 44.82)	-3.84 (-25.65, 17.99)
Body mass (per g)	**9.40e-3 (2.78e-3, 1.61e-2)**	**2.79e-2 (1.00e-2, 4.59e-2)**	**1.24e-2 (3.45e-3, 2.20e-2)**	**1.32e-2 (4.16e-3, 2.16e-2)**	4.06e-3 (-1.41e-2, 2.26e-2)	1.04e-4 (-1.50e-2, 1.55e-2)	4.22e-3 (-9.06e-3, 1.78e-2)
Dive order (per dive)	1.07e-2 (-2.59e-2, 4.81e-2)	**0.15 (4.11e-2, 0.26)**	**9.56e-2 (3.11e-2, 0.16)**	5.68e-2 (-2.45e-3, 0.12)	-8.00e-2 (-0.38, 0. 23)	-1.77 (-044, 0.11)	-0.20 (-0.78, 0.39)
Interaction Body mass and dive order	-8.91e-6 (-3.18e-5, 1.37e-5)	**-1.04e-4 (-1.72e-4, -3.41e-5)**	**-6.43e-5 (-1.04e-4, -2.46e-5)**	**-4.04e-5 (-7.92e-5, -2.61e-6)**	2.43e-5 (-1.71e-4, 218e-4)	8.12e-5 (-9.61e-5, 2.45e-4)	1.21e-4 (-2.44e-4, 4.82e-4)
ID	0.17	0.16	0.11	0.14	0.03	0.02	0.27
Location	0.14	0.19	0.11	0.11	0.01	0.00	0.34
Year	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dive date	0.06	0.06	0.05	0.05	0.00	0.00	0.19
Residual	0.63	0.59	0.72	0.71	0.96	0.97	0.19

Males NBD dives

Intercept	5.15 (-18.81, 28.94)	19.40 (-21.26, 62.21)	10.87 (-13.90, 34.86)	7.97 (-6.84, 21.98)	33.34 (-58.94, 115.41)	22.96 (-49.26, 97.11)	-0.48 (-11.54, 11.03)
Body mass (per g)	5.01e-3 (-7.6e-3, 1.74e-2)	9.09e-3 (-1.13e-2, 3.01e-2)	5.57e-3 (-7.51e-3, 1.64e-2)	4.45e-3 (-2.84, 1.19e-2)	5-96e-3 (-3.51e-2, 5.00e-2)	1.05e-2 (-2.85e-2, 4.72e-2)	1.11e-3 (-4.68e-3, 6.82e-3)
Dive order (per dive)	**0.16 (6.56e-2, 0.24)**	**0.28 (0.07, 0.48)**	**0.15 (2.14e-2, 0.28)**	**0.12 (5.65e-3, 0.23)**	**0.92 (0.39, 1.40)**	**1.12 (0.64, 1.57)**	-1.52e-3 (-0.52, 0.23)
Interaction Body mass and dive order	**-7.71e-5 (-1.20e-4, -3.03e-5)**	**-1.46e-4 (-2.50e-4, -3.88e-5)**	**-7.66e-5 (-1.44e-4, -1.07e-5)**	**-6.48e-5 (-1.20e-4, -5.08e-6)**	**-5.22e-4 (-7.74e-4, -2.53e-4)**	**-6.39e-4 (-8.78e-4, -3.86e-4)**	6.11e-5 (-1.28e-4, 2.47e-4)
ID	0.22	0.17	0.15	0.10	0.18	0.15	0.12
Location	0.18	0.13	0.14	0.11	0.07	0.08	0.42
Year	0.05	0.04	0.04	0.05	0.03	0.03	0.01

Dive date	0.22	0.21	0.17	0.10	0.04	0.00	0.17
Residual	0.34	0.44	0.51	0.65	0.72	0.74	0.29

b) Females WBD dives

	Max depth (m)	Dive duration (s)	Descending duration (s)	Ascending duration (s)	Bottom duration (s)	Pre-dive duration (s)	Post-dive duration (s)	Bout length (n)
Intercept	-10.80 (-25.07, 3.86)	-19.39 (-56.25, 17.44)	-3.72 (-14.66, 7.55)	-4.39 (-12.70, 3.94)	-6.74 (-22.47, 9.52)	5.83 (-17.94, 28.46)	3.75 (-23.60, 31.18)	1.80 (-6.52, 8.62)
Body mass (per g)	**1.21e-2 (3.10e-3, 2.09e-2)**	**3.38e-2 (1.17e-2, 5.52e-2)**	**9.58e-3 (2.78e-3, 1.61e-2)**	**9.00e-3 (3.87e-3, 1.39e-2)**	**1.14e-2 (1.38e-3, 2.08e-2)**	1.10e-2 (-3.10e-3, 2.52e-2)	1.27e-2 (-4.01e-3, 2.97e-2)	5.55e-4 (-3.59e-3, 5.39e-3)
Dive order (per dive)	**-5.49e-2 (-9.81e-2, -1.10e-2)**	1.86e-2 (-1.17e-4, 2.53e-5)	-4.31e-3 (-5.90e-2, 5.08e-2)	8.79e-3 (-3.23e-2, 4.66e-2)	6.58e-3 (-6.20e-2, 7.27e-2)	-8.83e-4 (-0.22, 0.22)	0.10 (-0.14, 0.35)	-9.21e-2 (-0.30, 0.10)
Interaction Body mass and dive order	2.78e-5 (-2.45e-7, 5.46e-5)	-4.26e-5 (-1.17e-4, 2.53e-5)	-6.04e-6 (-3.95e-5, 2.84e-5)	-1.18e-5 (-3.61e-5, 1.29e-5)	-1.93e-5 (-6.10e-5, 2.35e-5)	-2.47e-5 (-1.61e-4, 1.12e-4)	-8.79e-5 (-2.42e-4, 6.29e-5)	4.83e-5 (-7.05e-5, 1.77e-4)
ID	0.19	0.20	0.11	0.09	0.13	0.03	0.03	0.03
Location	0.17	0.21	0.05	0.13	0.08	0.04	0.04	0.73
Year	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dive date	0.03	0.02	0.01	0.01	0.02	0.00	0.00	0.07
Residual	0.62	0.56	0.84	0.77	0.77	0.93	0.93	0.17

Males WBD dives

Intercept	5.71 (-19.87, 28.89)	19.94 (-23,70, 67.22)	8.37 (-11.70, 27.82)	8.27 (-3.64, 21.19)	2.74 (-9.90, 15.21)	32.24 (-41.80, 103.84)	33.93 (-49.56, 116. 27)	3.31 (-3.18, 9.92)
Body mass (per g)	5.72 (-6.15e-3, 1.83e-2)	1.43e-2 (-9.31e-3, 3.67e-2)	5.75e-3 (-4.60e-3, 1.58e-2)	3.15e-3 (-3.32e-3, 9.20e-3)	5.53e-3 (-1.14e-3, 1.21e-2)	7.06e-3 (-2.97e-2, 4.51e-2)	5.88e-3 (-3.60e-2, 4.87e-2)	-6.49e-4 (-4.00e-3, 2.60e-3)
Dive order (per dive)	**0.18 (0.12, 0.23)**	**0.22 (9.40e-2, 0.34)**	**0.13 (6.32e-2, 0.20)**	**0.12 (6.15e-2, 0.17)**	-5.09e-2 (-0.13, 3.36e-2)	0.16 (-0.11, 0.43)	0.10 (-0.19, 0.42)	3.61e-2 (-0.18, 0.26)
Interaction Body mass and dive order	**-9.44e-5 (-1.22e-4, -6.71e-5)**	**-1.41e-4 (-2.03e-4, -7.99e-5)**	**-7.50e-5 (-1.09e-4, -4.00e-5)**	**-6.56e-5 (-9.27e-5, -3.80e-5)**	8.96e-6 (-3.51e-5, 4.95e-5)	-1.23e-4 (-2.67e-4, 1.34e-5)	-8.66 (-2.51e-4, 5.99e-5)	-3.87e-5 (-1.51e-4, 7.18e-5)
ID	0.26	0.24	0.21	0.15	0.10	0.18	0.21	0.06
Location	0.15	0.12	0.13	0.16	0.02	0.14	0.13	0.37
Year	0.01	0.02	0.03	0.02	0.01	0.03	0.03	0.00
Dive date	0.20	0.19	0.08	0.06	0.02	0.01	0.01	0.08
Residual	0.34	0.44	0.55	0.61	0.86	0.64	0.62	0.48

In males there was a positive effect of dive order on depth and dive duration in both dive types, and with little effect on surface durations (Table 4). This suggests that the differences in dive parameters between the two dive types became smaller for longer dive bouts (i.e. for bouts of 110 dives, male WBD and NBD dives would on average be at approximately the same depth of 16.5m). In both dive types for males, the effect of body mass showed a significant interaction with dive order (Table 4), suggesting an upper threshold of a certain number of consecutive dives after which body mass had little effect. WBD dive depth was deeper than NBD dives for males, but again there was no significant effect of body mass. Seemingly, male dives required deeper and perhaps more random variation in depth not associated simply with the effects of body mass alone.

Females showed a positive effect of dive order in NBD dive duration and descending duration (Table 4a), but with an interaction between body mass and dive order of negative effect. Females also had a significantly negative effect of dive order in WBD dive depth (Table 4b), translating to -5.5m difference (-5.49e-2, C.I.: -9.81e-2, -1.10e-2) between the first and last dive in a bout constituting of 100 dives. Female body mass had a large positive effect on all dive parameters whenever the effect was significant. For example, body mass had a positive effect on maximum depth of NBD dives in females (Table 4a), where the maximum depth increased by 0.0008m per gram, which translates to an overall effect of mass changing dive depths from 3.87m to 7.89m, a range of 4.02m within the body mass range for female birds in this sample. Female WBD dives were deeper than NBD dives, ranging from 5.35m to 9.76m (body mass specific) increasing linearly as body mass increased. Dive durations also increased with body mass in both NBD and WBD dives (Table 4a &b) for female birds. Although this largely reflected the effects (above) in maximum dive depth, the effects of body mass on dive durations seemed less affected by random noise generated due to prey pursuits during WBD dives.

Heavier birds of both sexes chose longer lasting NBD and WBD dives. Female NBD dive durations was estimated to range from 15.19s for the lightest individuals to 27.42s for the heaviest, with a mean of 21.13s. Male NBD dive durations averaged 29.45 s with no effect of body mass. Females dive durations were estimated to increase for WBD, to 25.54 s for the smallest individuals and 40.15 s for the largest ones, and mean body mass dive duration of 32.70 s (increase of 11.57s from NBD dives). Male WBD dive duration increased to 36.17s for the smallest individuals (1660g), 48.57s for the largest one (2280g) and 41.37s (increase of 11.92s) for mean mass. The largest female bird is thus estimated to choose dive durations equal to male birds in the same weight class, emphasising that the effect of sex cannot be distinguished from the effect of body mass. In fact, the effect of mass completely overlapped the effect of sex on maximum depth and the different dive durations, when ran as a strictly linear effect for females vs. males (Appendix, Table S5). Where the effect of sex on maximum depth in Table 2 was 4.88m, the effect of body mass for a weight difference of 300g (mean difference between males and females) were 4.34m. The same effect was found for dive duration, where the sex difference was 11.15s in total dive duration and 3.3s in bottom duration, a 300g body mass difference meant 13.5s and 3.3s difference, respectively. This was not the case for surface duration however, where pre- and post-dive duration had no direct effect of mass, but a 13.33s and 13.26 difference between the sexes.

There was no effect of body mass on surface durations when it was entered into models on its own, but there was a distinct sex difference (Table S5). In Table 4a and b there proved to be an effect of dive order and an interaction between dive order and body mass on surface durations for male WBD dives, only (i.e. no effect on male NBD nor on female dives in general). However, there was a strong dive order effect in all cases when it was on its own in the models (Table S4). There must therefore be another effect on surface durations that was not included in the models (e.g. an effect of temperature in the sea water, total bout length, location, prey abundance).

Section 1C: Descent and Ascent Speed

As the analysis above showed, there were distinct differences between descending and ascending durations (see Table 2, Figs 4c and 4d). NBD dives seemed to reach shallower depths in the same descent duration as deeper WBD dives, indicating different speeds in the two types of dives possibly indicating that WBD dives are active hunting chases and NBD dives are slower information gathering or sampling dives. Body mass should play a significant part in movement through the water and was therefore included in the models testing for such effects of speed (Table 5, Fig.7), where the effects of speed of descending and ascending travel during dives of different depths were estimated by exploring variation in maximum depth due to travel duration and body mass.

The effect of descent and ascent durations on maximum depth was close to linear for NBD dives and decelerating for WBD dives (Table 5; Fig.7a and b). This suggests that NBD dives involved simple trips straight down and straight back up, with no changes in swimming speeds with depth. The deceleration apparent in WBD dives suggests that the end of the deeper descent and the start of the ascent involved a levelling off of the dive trajectory before such lateral movement was classified by our algorithm as bottom duration (see Methods). Most importantly, the linear travel duration effect on the curves were in all cases larger for WBD dives than for NBD dives (Table 5a & b) and the polynomial decrease in WBD dives only affected dives at large depths. In conclusion; there was definitely a difference in speed between the two dive types, and WBD dives were faster than NBD dives, giving more support to the idea of these as active hunting/chasing dives.

Body mass had a positive effect on the maximum depth-descending relationship for females NBD dives, by $0.003 \mathrm{ms}^{-1}$ (C.I.:8.5e-5, 7.8e-3). In contrast, when engaged in WBD dives there was a clear deceleration for the greater depths, probably as the birds gradually chose a more horizontal movement (maybe due to reaching the sea floor or the lower limit of prey availability), possible even moving further horizontally than vertically, but still gaining enough depth to be counted as a part of descendant duration. Body mass still played a role, with a slightly larger positive effect as the depth increased, of $0.004 \mathrm{m\ s}^{-1}$ (C.I.: 8.5e-5, 7.8e-3). There was no clear effect of body mass on the male birds, reflecting the findings in Section 1B. It is necessary to mention that interactions between both body mass and body mass squared with the dive parameters and dive parameters squared were significant, and sometimes with effect sizes equal to the effect of mass alone, for both sexes in most cases, meaning that the body mass effect here was complex and difficult to interpret as simply an effect of buoyancy.

Table 5: The effect on maximum depth of (a) descending and (b) ascending durations, separated by sex and dive type (no bottom duration NBD versus with bottom duration WBD dives). Note that the non-linear duration term was only included when significant. Mixed effect models included identity, location, year and dive date as random effects, which are given as proportions of total variation explained. Fixed effects are given as effect sizes (for non-standardized values) with 95% CIs. Bold numbers for significant values, except in intercepts.

a) Effect of descending duration on maximum depth

	Female NBD	Female WBD	Male NBD	Male WBD
Intercept	-3.86 (-8.64, 0.86)	-6.02 (-12.32, 0.27)	-2.60 (-13.58, 7.71)	-4.31 (-16.59, 7.92)
Descending duration (s)	**0.36 (0.34, 0.37)**	**0.83 (0.80, 0.85)**	**0.63 (0.60, 0.65)**	**0.90 (0.87, 0.92)**
Descending duration^2 (s^2)	**0.002 (0.001,0.002)**	**-0.01 (-0.01, -0.009)**	**-0.002 (-0.002, -0.001)**	**-7.5e-3 (8.0e-3, -6.9e-3)**
Body mass (per g)	**0.003 (4.1e-4, 6.3e-3)**	**0.004 (8.5e-5, 7.8e-3)**	0.003 (-0.002, 0.009)	3.8e-3 (-2.3e-3, 0.01)
ID	0.09	0.09	0.15	0.22
Location	0.04	0.08	0.25	0.15
Year	0.00	0.00	0.04	0.02
Dive date	0.05	0.05	0.06	0.12
Residual	0.82	0.78	0.50	0.50

b) effect of ascending duration on maximum depth

	Female NBD	Female WBD	Male NBD	Male WBD
Intercept	-2.83 (-7.09, 1.62)	-5.46 (-12.59, 1.95)	-2.75 (-16.62, 10.08)	-6.33 (-19.75, 8.01)
Descending duration (s)	**0.39 (0.37, 0.41)**	**1.01 (0.98, 1.05)**	**0.68 (0.65, 0.72)**	**1.07 (1.03, 1.11)**
Descending duration^2 (s^2)	**0.002 (0.001, 0.003)**	**-0.02 (-0.022, -0.021)**	**-0.002 (-3.0e-3, -1.4e-3)**	**-0.01 (-0.013, -0.011)**
Body mass (per g)	**0.003 (4.6e-6, 5.3e-3)**	0.004 (-9.7e-4, 0.01)	0.003 (-0.003, 0.01)	5.4e-3 (-2.0e-3, 0.01)
ID	0.07	0.09	0.22	0.28
Location	0.04	0.10	0.20	0.08
Year	0.00	0.00	0.04	0.03
Dive date	0.04	0.05	0.07	0.10
Residual	0.85	0.75	0.48	0.51

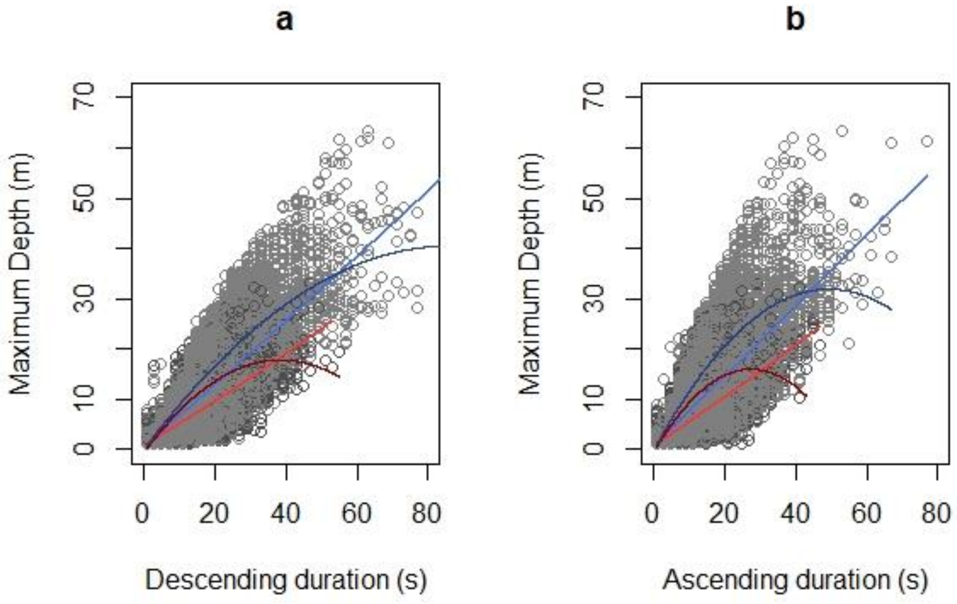


Fig 7: The effect on maximum depth of (a) Descending duration and (b) Ascending duration, separated by dive type (no bottom duration NBD [light colours]; With bottom duration WBD [dark colours]) and sex (female [red]; male [blue]) - see Table 5.

Section 1D: Additional Sources of Variation in the Dive Parameters

In general, the random effects in the models for results in Tables 2, 3,4 and 5 such as individual identity (ID) explained a substantial proportion of the variation in all parameters (between 0.11 and 0.30), suggesting that individual differences and/or differences in state determined their foraging behaviour in terms of the characteristics of their diving behaviour. Interestingly, nest ID (i.e. individuals belonging to the same nest or pair) was tested as an additional random effect, but it rarely explained more than 0.0002% of the variation in dive parameters, suggesting that conditions related to the nest, brood or pair explained fairly little of the variation in foraging behaviour of individuals -see Discussion. For simplicity, nest ID was therefore removed from all models (see Methods). The differences in preferred foraging tactics between individuals therefore appear to be explained by the large individual ID random effects, which was larger for WBD dives compared to NBD dives where all individuals behaved very similarly.

Perhaps unsurprisingly, location also explained a lot of variation in dive depth (2-25%) and thus dive duration (10-25%) and descending (4-25%) and acceding durations (4-20%), probably as a result of shallow areas inshore limiting dive depths, and thus travel time, but maybe also due to differences in prey depths at different locations. Location explained a substantial proportion of bout lengths, suggesting a large variation in quality of foraging patches.

While year had only a minor effect, there was some effect of dive date within each season (3-9%), mostly again on dive depth and thus travel durations, and especially for bout length. Although year and date will have been somewhat confounded with individual identity in these data (i.e. each individual only measured one year), year also lost most of its explanatory value to the dive date (3-12%). Due to the large effect of dive date in the random effects (Tables 2-5), it is of interest to look closer into day as a linear (fixed) effect within each season to get a clearer picture of where this seasonal change occurs and the magnitude of it.

In the analysis any variation due to the different 25 days per season are accounted for as the random effect of dive date. Determining the effect size of seasonal changes on each of the main parameters were important, however, to establish whether early versus late breeders differed, for example due to increased brood demand and/or change in prey availability, and to establish whether this variation was simply due to changes in body mass over the season (e.g. across early versus late nesting individuals) rather than other types of season effects.

Table 6 shows that date within the season had a consistent and substantial impact on all dive parameters, with the possible exception of females during NBD dives. Interestingly, females were affected positively by day within the season, whereas males were negatively affected (Table 6; Fig.8). It therefore appears that the sexes differed most in their dive behaviour early within each breeding season, and gradually converged to end each season with quite similar dive parameters.

Table 6: The fixed effect of day within the season and body mass (linear and curvilinear terms) on the different dive parameters, separated by sex for (a) no bottom duration (NBD) and (b) with bottom duration (WBD) dive types. Dive day represents the day within the total length of all seasons combined, discretely from the earliest (day 1) to the latest (day 25). Mixed effect models included identity, location, year and dive date as random effects, which are given as proportions of total variation explained. Fixed effects are given as effect sizes (for non-standardized values) with 95% CIs. Bold numbers for significant values, except in intercepts. Curvilinear effects were removed from models whenever non-significant, along with any linear effects as well when justified by protocols of model reduction (see Methods).

a) Females NBD dives

	Max depth (m)	Dive duration (S)	Descending duration (S)	Ascending duration (S)	Pre-dive duration (S)	Post dive duration (S)
Intercept	-9.33 (-20.17, 1.77)	-418.8 (-761.6, -74.24)	-183.79 (-348.98, -28.17)	-11.11 (-24.95, 1.60)	11.18 (-19.73, 40.61)	31.92 (3.32, 58.39)
Dive day	0.04 (-0.10, 0.17)	-1.97 (-0.38, 0.36)	-0.03 (-0.24, 0.15)	0.05 (-0.13, 0.23)	0.20 (-0.21, 0.61)	**-2.13 (-3.95, -0.44)**
Dive day^2	-	-	-	-	-	**0.08 (0.02, 0.14)**
Body mass (per g)	**0.009 (0.002, 0.02)**	**5.12 (0.095, 0.092)**	**0.22 (0.01, 0.44)**	0.01 (-0.13, 0.02)	0.004 (-0.01, 0.02)	-7.62e-5 (-0.02, 0.02)
Body mass^2 (per g^2)	-	-	**-6.38e-5 (-1.29e-4, -2.81e-6)**	-	-	-
ID	0.19	0.18	0.13	0.15	0.03	0.02
Location	0.14	0.17	0.11	0.09	0.01	0.00
Year	0.00	0.00	0.00	0.00	0.00	0.00
Dive date	0.05	0.06	0.05	0.04	0.00	0.01
Residual	0.62	0.59	0.72	0.71	0.95	0.97
Males NBD dives						
Intercept	28.87 (22.73, 35.60)	67.34 (55.26, 78.73)	35.38 (28.39, 41.91)	26.78 (21.96, 31.81)	60.30 (43.81, 79.03)	60.28 (44.66, 77.10)
Dive day	**-1.07 (-1.35, -0.77)**	**-2.27 (-2.87, -1.64)**	**-1.16 (-1.51, -0.81)**	**-0.75 (-1.03, -0.50)**	**-1.12 (-2.07, -0.22)**	**-1.15 (-2.00, -0.29)**
ID	0.33	0.30	0.24	0.17	0.17	0.14
Location	0.18	0.13	0.14	0.10	0.07	0.08
Year	0.06	0.05	0.05	0.04	0.03	0.00
Dive date	0.06	0.06	0.06	0.05	0.01	0.03
Residual	0.37	0.46	0.51	0.65	0.73	0.75

b) Females WBD dives

	Max depth (m)	Dive duration (s)	Descending duration (s)	Ascending duration (s)	Bottom duration (s)	Pre-dive duration (s)	Post dive duration (s)
Intercept	-13.01 (-25.47, 0.40)	-52.81 (-946.27, -140.44)	-4.32 (-15.15, 5.94)	-115.33 (-214.56, -12.75)	-181.53 (-341.02, -15.34)	3.41 (-20.65, 28.22)	-1.13 (-28.59, 27.16)
Dive day	**0.17 (0.06, 0.29)**	0.28 (-0.03, 0.57)	0.08 (-0.02, 0.18)	**0.12 (0.03, 0.27)**	-0.02 (-0.17, 0.15)	0.33 (-20.65, 28.22)	**0.42 (0.09, 0.76)**
Body mass (per g)	**0.01 (0.004, 0.02)**	**0.65 (0.18, 1.16)**	**0.009 (0.003, 0.016)**	**0.14 (0.02, 0.27)**	**0.23 (0.02, 0.42)**	**9.00e-3 (-5.26e-3, 0.02)**	0.01 (-0.01, 0.03)
Body mass^2 (per g)	-	**-1.89e-4 (-3.47e-4, -4.12e-5)**	-	**-4.11e-5 (-7.87e-5, -2.84e-6)**	**-6.51e-5 (-1.26e-4, -3.85e-6)**	-	-
Id	0.21	0.21	0.12	0.11	0.14	0.03	0.03
Location	0.22	0.30	0.09	0.16	0.11	0.07	0.08
Year	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dive date	0.02	0.01	0.00	0.00	0.01	0.00	0.00
Residual	0.55	0.48	0.79	0.72	0.74	0.90	0.89
Males WBD dives							
Intercept	27.76 (23.53, 32.08)	62.58 (51.73, 73.63)	27.68 (23.73, 31.78)	21.33 (18.64, 24.06)	18.40 (15.52, 21.10)	65.45 (51.28, 80.33)	62.17 (46.99, 77.43)
Dive day	**-0.83 (-1.01, -0.65)**	-0.18 (-1.62, 1.17)	**-0.60 (-0.80, -0.41)**	**-0.50 (-0.63, -0.36)**	**-0.34 (-0.50, -0.17)**	**-1.34 (-2.06, -0.68)**	**-1.17 (-1.89, -0.46)**
Dive day^2	-	**-0.05 (-0.10, -0.005)**	-	-	-	-	-
Id	0.39	0.34	0.27	0.20	0.11	0.17	0.19
Location	0.17	0.13	0.12	0.15	0.02	0.15	0.14
Year	0.01	0.01	0.03	0.01	0.00	0.03	0.03
Dive date	0.03	0.03	0.12	0.01	0.01	0.01	0.01
Residual	0.40	0.50	0.56	0.62	0.86	0.64	0.63

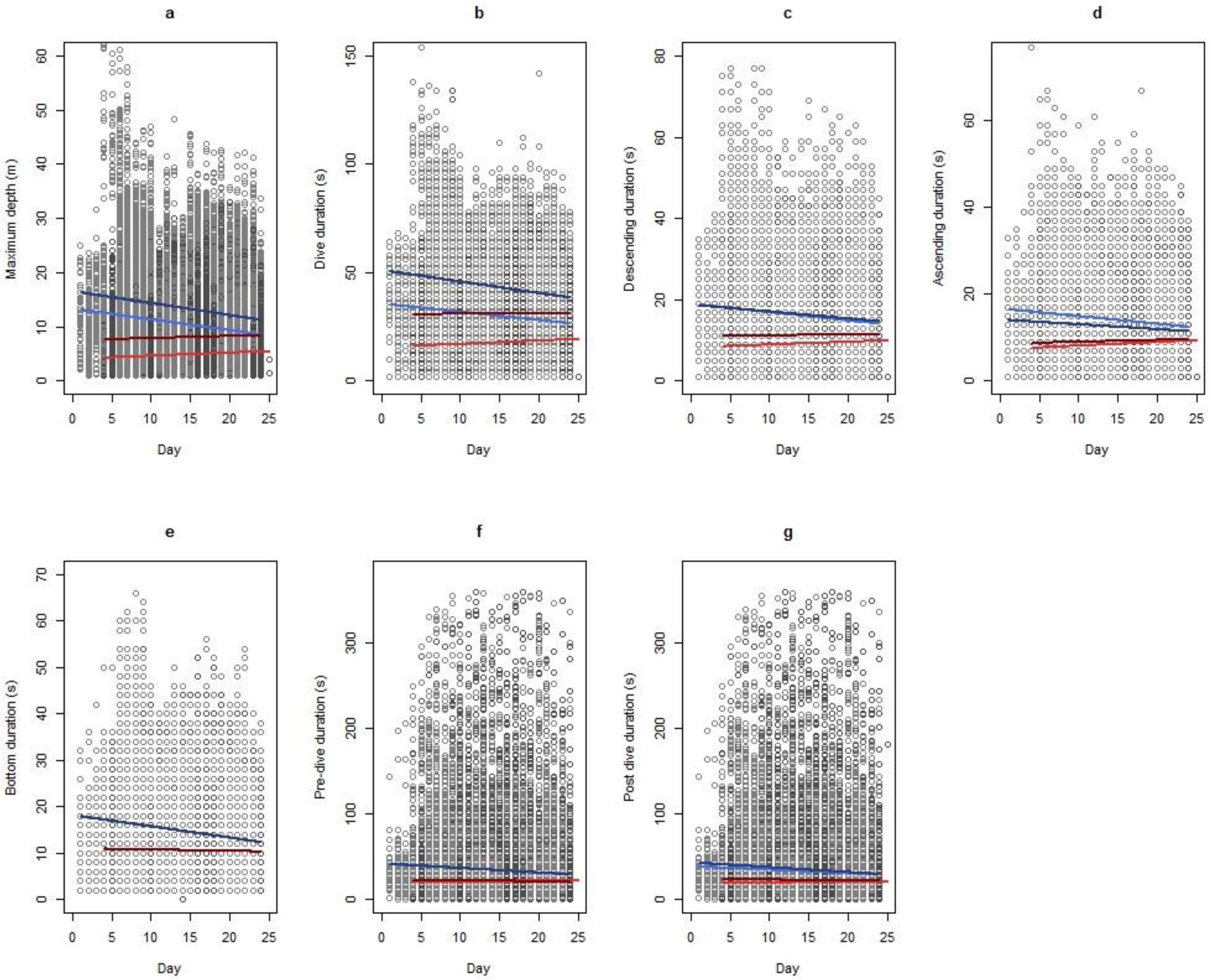


Fig 8: The effect of day within season (0 = 22nd June) over the 6 years of data on the different dive parameters, separated by dive type (light colours= no bottom duration NBD; dark colours= with bottom duration WBD) and sex (female= red; male= blue). (a) Maximum depth, (b) Dive duration, (c) Descending duration, (d) Ascending duration, (e) Bottom duration, (f) Pre-dive duration and (g) Post dive duration (see Table 6).

During NBD dives, female birds did not seem to be significantly affected by the day of dive (Table 6a), although there was a positive effect of body mass on maximum depth (Fig.8a), dive duration (Fig.8b) and descending duration (Table 6c). Notable, the effect of day was positive for pre-dive duration, but negative for post-dive surface duration (Table 6a; Fig. 8g). In females WBD dives, there was a significantly positive effect of day on maximum depth, ascending duration and post-dive surface duration (Table 6b), as well as a positive effect of body mass on all of the parameters. The findings indicate a season change in physical properties of the birds (i.e. body mass) or their environment (i.e. vertical movement of prey or brood demand).

There was a decrease in males maximum depth, dive duration, descending and ascending duration with dive day, in NBD dives. However, the estimation may be somewhat skewed due to the two shallow dives on the last day of season which could pull the average down. In males WBD dives the maximum depth decreased somewhat less than in NBD dives (Table 6a-b). Male birds decreased their surface durations both before and after dives with dive day for both dive types.

The main positive effect on females dive parameters in Table 6a-b was body mass, and in several parameters there was a visible increase in values from early to late dive days (Fig. 8a-g), indicating an increase in body mass over season. Interestingly, male birds showed an opposite pattern, with a decrease in most of the parameter values with dive day (i.e. time of season), but no effect of body mass. This again emphasizes the effect body mass has on diving properties (although, possibly with an interaction or effect of dive order that was not tested here), here reflected in change over season. Female shags may either increase body mass over the season and be in general heavier in late summer, or late breeders especially may have had more time to become heavier before breeding.

SECTION 2:

We considered the general patterns in diving behaviour of males and females in NBD and WBD dives in Section 1. In this second part of the result the MVT were adapted to test certain predictions concerning the optimal dive behaviour based on issues such as gas exchange during surface durations between dives (see Introduction).

2A.1: Exponential relationships between dive time and dive cycles

The dive cycle consists of consecutive dive durations and their connected surface duration, and it constitutes an important composite parameter for testing simple MVT predictions (see Introduction and Stephens *et al.* 2007). To test the relative importance of surface durations occurring before or after the dive, we distinguished between dive cycles before (DCB), which includes the surface duration before a dive (pre-dive surface duration), and dive cycles after (DCA) that include the surface duration after a dive (post dive surface duration).

As dive duration increased, DCB and DCA durations all showed an exponential increase, confirming that the birds adjusted their surface durations to the accelerating costs of increasing dive durations (Table S6a-d, Figs 9a-d). These results reflect how longer dives lead to a non-linear increasing surface durations and therefore also dive cycle durations to replenish O_2 stores resulting in diminishing returns for longer and longer dives (see Introduction).

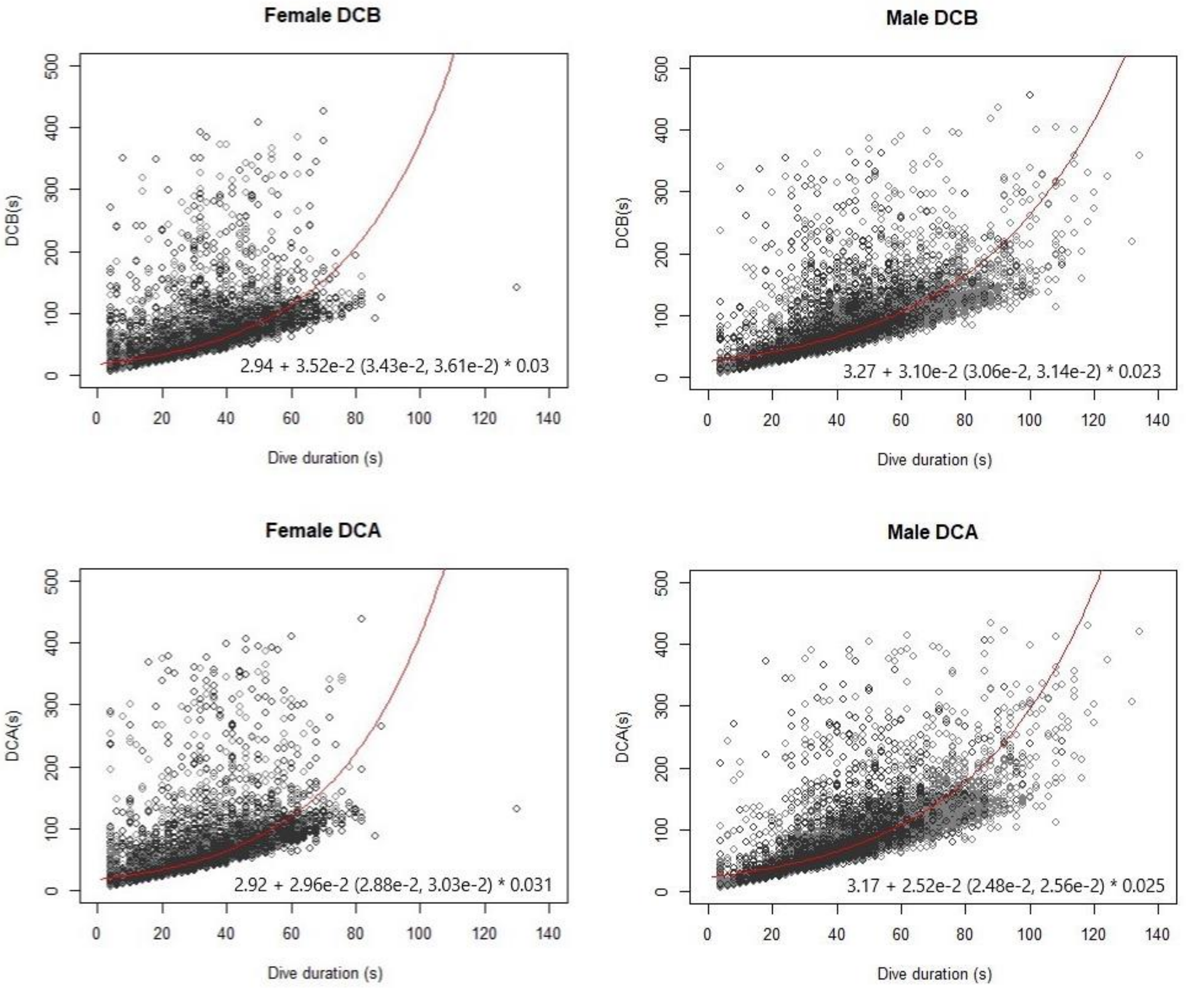


Fig 9: The exponential effect of dive duration on dive cycles (dive durations plus surface durations) using surface times before (DCB) versus after (DCA) in with bottom duration (WBD) dives separated by sex, model given in the plot. See Table S6.

The curves in Fig. 9 all appear to result in rather non-homogenous residuals in that there is a lower limit to the densest cluster of points in each case that appears to be more or less linear. This is due to the y-axis dive cycle values being a composite measure that include those of dive duration on the x-axis – i.e. values cannot exist below the diagonal of equal x- and y-axis values. Thus, a better statistical understanding of these effects (i.e. one in which the effect of body mass could also be legitimately explored) would perhaps be gained by looking at the more simple relationships between surface duration and dive duration, or between travel duration and bottom duration (See Fig. 10).

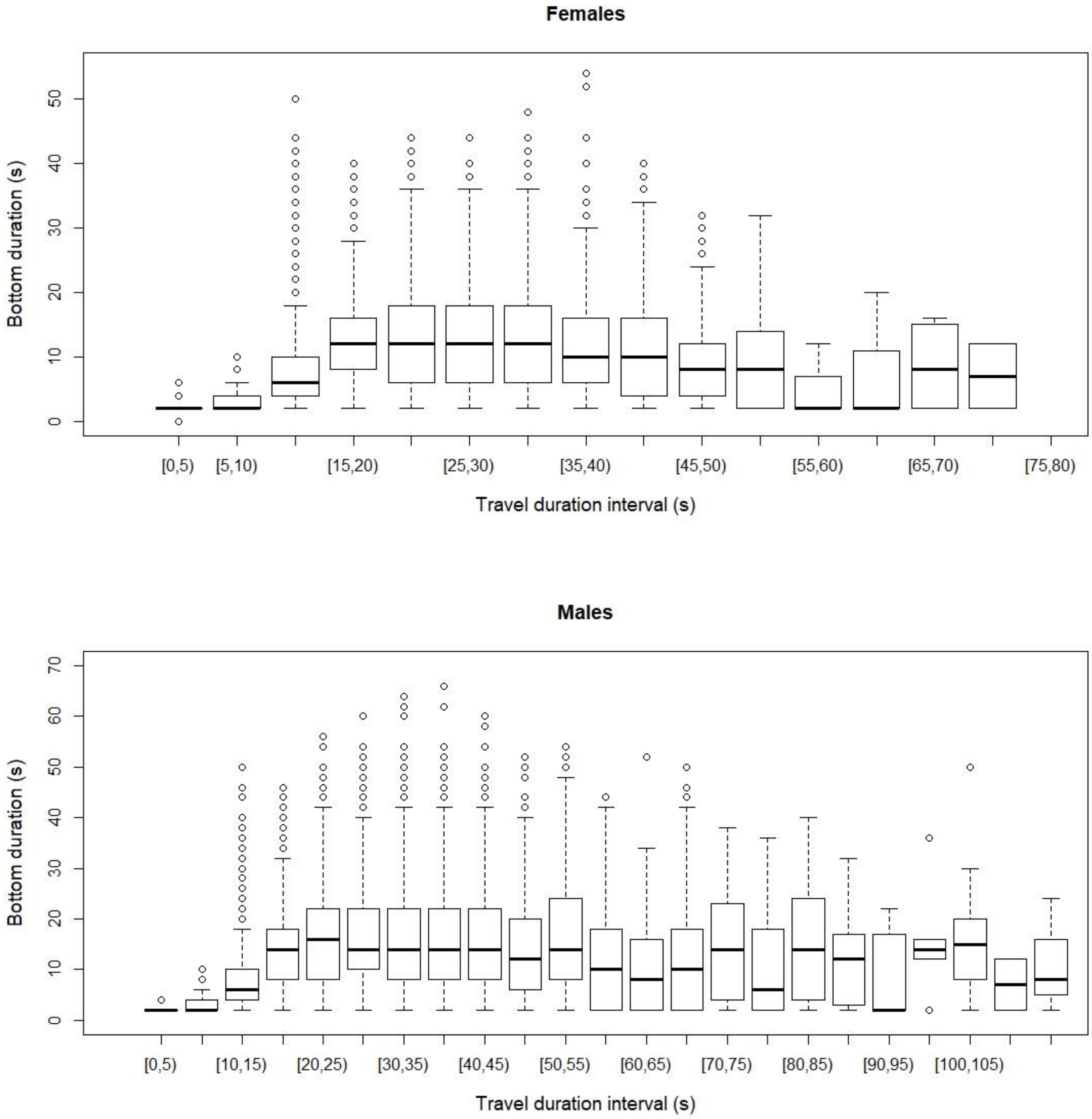


Fig 10: The effect of travel duration (separated into 10s categories) on bottom duration (median values, interquartile ranges and 95% CI plus outliers) separated by sex - see Table S7.

Another way to approach the MVT prediction of C. W. Clarke (Stephens *et al.* 2007) would be to test whether a peak in bottom durations exists for a range of travel durations, presumably reflecting the optimum value that maximizes active foraging bottom time against the travel time needed to get there. There should also be interactions between this effect and body mass (i.e. aerobic capacity) according to the MVT.

As expected, there was a non-linear change in bottom duration as a response to increased travel duration (Fig. 10). Shorter travel durations had shorter to medium bottom durations, but as the travel durations became longer the time spent actively foraging increased to compensate for the increased investment At a certain point, however, the length of the travel started to have a decreasing effect on the bottom duration, presumably because there was a maximum dive duration limit that had to be divided between the two activities as a trade-off, within the trade-off between prey investment and surface duration. The over-all result suggests that there were deviations on either side of the optimal bottom duration that resulted in the vast majority of dives that did not maximize bottom duration for a given travel duration based on simple MVT predictions.

2A.2: The predicted bottom duration given by optimal dive duration

The correlations between the MVT predicted bottom duration (see Introduction and Stephens *et al.* 2007) and the observed bottom durations (Fig. 11a-b), based upon the known travel (descent plus ascent) travel durations, were 0.58 for both DCB and DCA in females, and 0.59 and 0.62 for males, respectively. However, there were some very short surface durations for a lot of the shorter dive durations, possibly reflecting specific types of errors in the data set that are hard to exclude (see Discussion). Therefore, the tangent to the curves in Fig.9a-d (see Introduction and Stephens *et al.* 2007) for dive durations shorter than 33s returned a negative x-intercept, thus predicting negative travel durations. It is therefore possible that the low correlations in Fig. 11a-b are due to these inaccuracies in the predictions at lower dive durations. However, as Fig. 11a-b shows, the most substantial scatter of points away from any line of correlation involves the longer bottom durations, perhaps reflecting an increasing source of variation in the bottom durations of individual dives with longer and longer hunts/chases of prey.

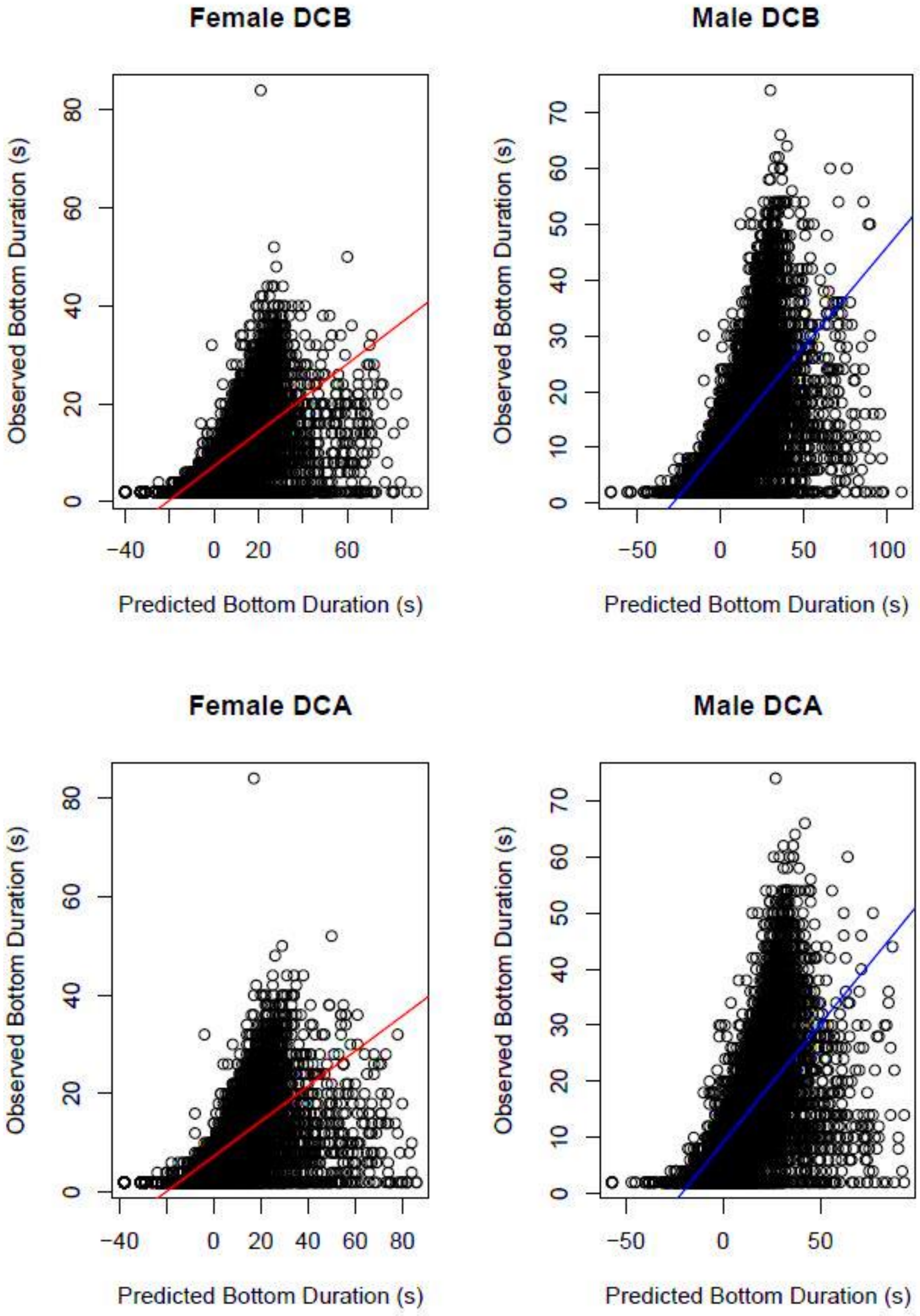


Fig. 11: The correlation between observed bottom duration (s) and predicted bottom duration (s) in WBD dives for DCB and DCA separated by sex (R2: 0.58, Female DCB; 0.58, female DCA, 0.59, male DCB, 0.62, male DCA).

2B: Statistically identifying maximal bottom durations

The position of the peak in the effect of travel duration on responding bottom duration (Fig.10) can be used to indicate whether an animal mainly depletes its respiratory O2-stored before switching to blood/tissue stores (i.e. switch metabolism, see introduction) during a dive (see Introduction). An attempt to test this relationship was conducted by running a piecewise linear regression looking for multiple lines that indicated changing directions within the observations (Fig. 12). There was found to only be one certain peak with a slowly decelerating tail in both female and male bottom durations (Fig. 12, see Appendix Table S8). Break point for females were 19.80 (20.02, 17.60), R2 for females were 0.72; Break point for males were 20.57 (20.24, 20, 91), R2 for males were 0.70. See Table SX, Appendix. This supports the assumption that switch metabolism between air sac stores and blood stores of O_2 provide a good explanation for shag dive behaviour (see Discussion). Further, the trade-off between bottom and travel duration became clear. Up to the break point, bottom duration increased with travel duration, suggesting that O2 in blood/tissue starts to become depleted, leading to a decrease in bottom duration for any further time spent foraging

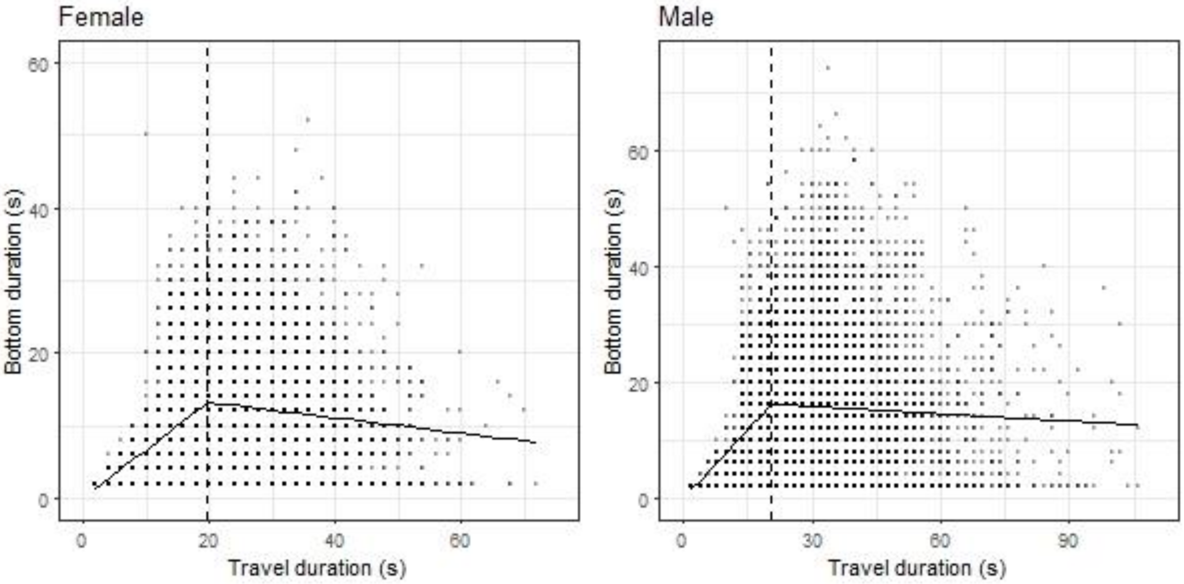


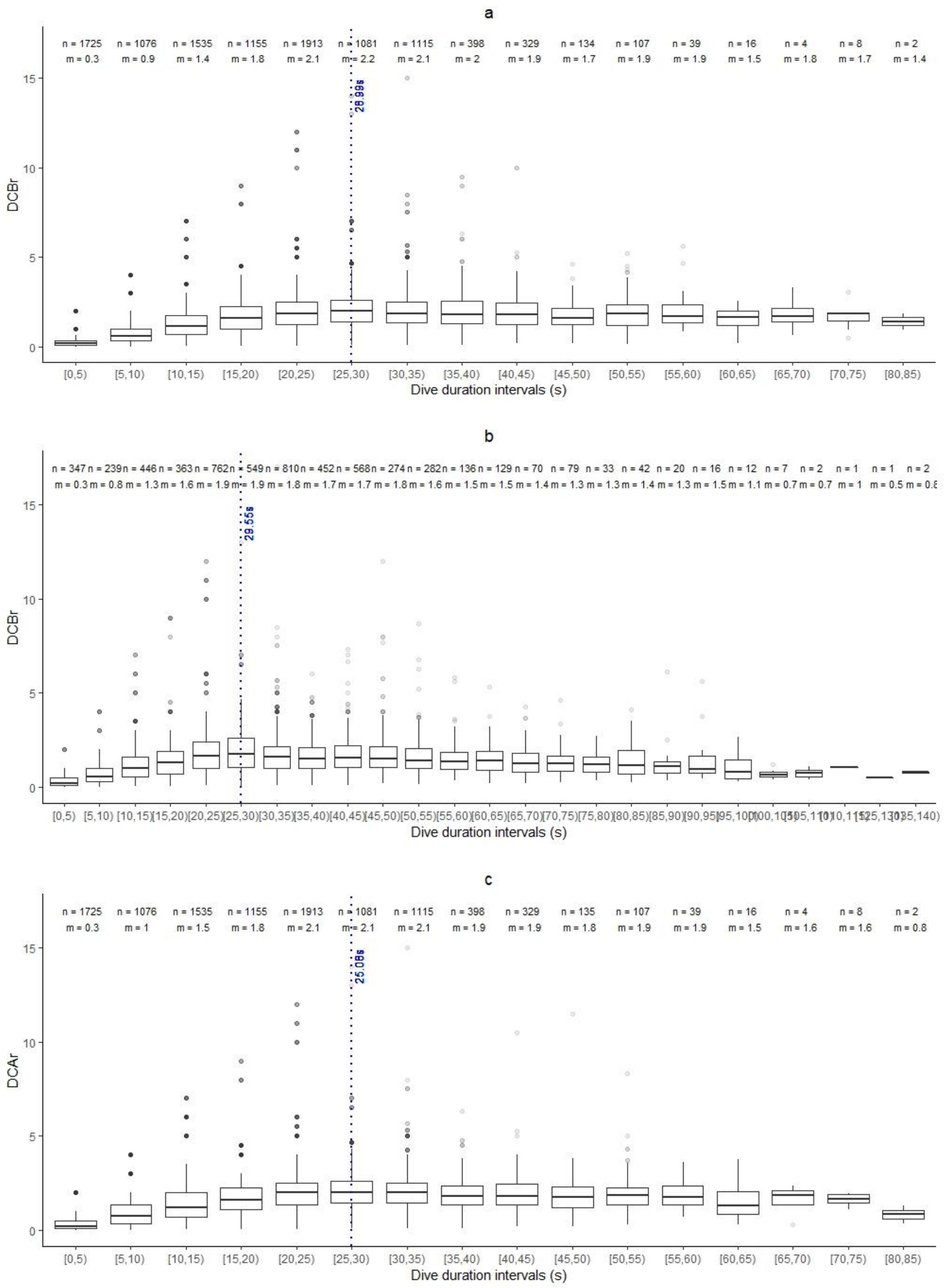
Fig. 12: The effect of increasing bottom duration with increased travel duration, indicated by piecewise linear regression. The break point of regression line (indicated by vertical stippled lines) for females were at travel durations of 19.80s (20.02, 17.60) and bottom duration of 12.49s (C.I.: 12.40, 12.56), R2 for females were 0.72; Break point for males were at travel duration of 20.57s (20.24, 20, 91) and bottom duration of 15.55s (C.I.: 15.47, 15.63), R2 for males were 0.70. See Table S8, Appendix.

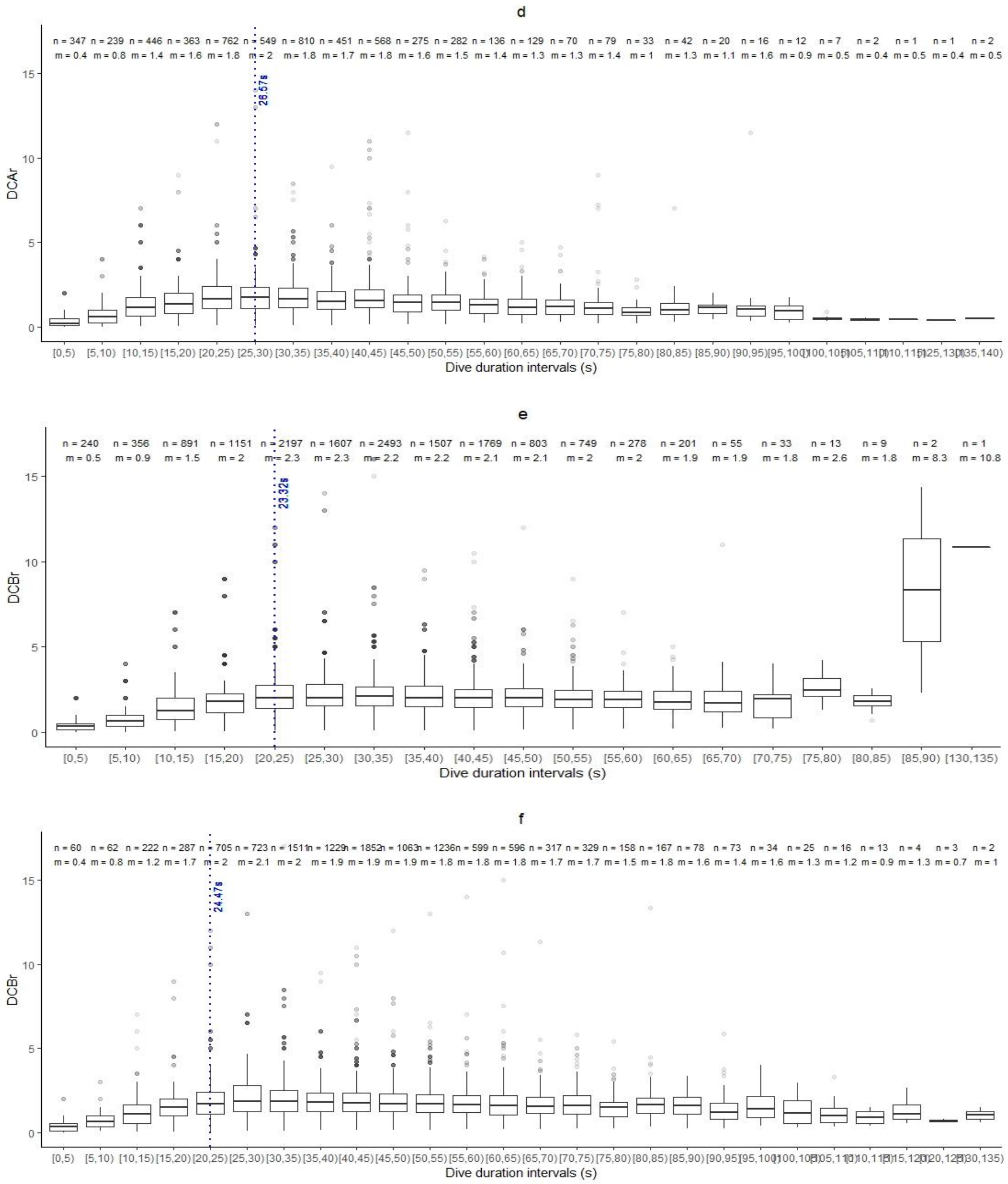
Now that the effect of travel duration on bottom duration, as well as the observed optimality in bottom duration has been set, the most elucidating analysis, on the *dive cycle ratio*, should be attended.

2C Dive duration to surface duration-ratio

A further and more sophisticated test of MVT predictions for shag behaviour in dive durations and surface durations involves the ratio of dive duration to surface duration (see Introduction and Walton *et al.* 1998). Therefore, the dive cycles using surface times before and after each dive were instead investigated here with ratios of dive duration to surface duration, using surface times before (DCBr) and after (DCAr) the dive. If our assumption of NBD dives as information sampling and WBD dives as hunts is correct, a trade-off between air sac and blood O_2 stores should be evident, by NBD dives ending closer to the peak ratio, while WBD dives, driven by the trade-off between catching prey and decreasing surface duration, should end at a later point in time (See Introduction).

Segments of linear regressions were divided by most likely break points (estimated by log-likelihood) -See Methods. The linear piecewise regression (Table 7c) estimated break points in dive duration that fitted neatly within the range of peaking ratio qualitatively estimated from ratio interval plots (See Table 7b) but giving a much more elegant answer to where in dive duration the peak ratio appears, as well as to compare the optimality in behaviour. The piecewise linear regression (Table 7c) had a tendency to estimate the peak to the lower end of the range of estimates in Table 7b. This may be partly due to the grouping and the peaks being borderline values within their interval, but probably also due to the lack of correction for nested data, as the method didn't allow random effects. The nesting does not take number of observations in each individual into consideration, thus smaller individuals with longer dive bouts will be over-represented.


a
n = 1725 n = 1076 n = 1535 n = 1155 n = 1913 n = 1081 n = 1115 n = 398 n = 329 n = 134 n = 107 n = 39 n = 16 n = 4 n = 8 n = 2
m = 0.3 m = 0.9 m = 1.4 m = 1.8 m = 2.1 m = 2.2 m = 2.1 m = 2 m = 1.9 m = 1.7 m = 1.9 m = 1.9 m = 1.5 m = 1.8 m = 1.7 m = 1.4
28.99s
DCBr
0
5
10
15
[0,5) [5,10) [10,15) [15,20) [20,25) [25,30) [30,35) [35,40) [40,45) [45,50) [50,55) [55,60) [60,65) [65,70) [70,75) [80,85)
Dive duration intervals (s)
b
n = 347 n = 239 n = 446 n = 363 n = 762 n = 549 n = 810 n = 452 n = 568 n = 274 n = 282 n = 136 n = 129 n = 70 n = 79 n = 33 n = 42 n = 20 n = 16 n = 12 n = 7 n = 2 n = 1 n = 1 n = 2
m = 0.3 m = 0.8 m = 1.3 m = 1.6 m = 1.9 m = 1.9 m = 1.8 m = 1.7 m = 1.7 m = 1.8 m = 1.6 m = 1.5 m = 1.5 m = 1.4 m = 1.3 m = 1.3 m = 1.4 m = 1.3 m = 1.5 m = 1.1 m = 0.7 m = 0.7 m = 1 m = 0.5 m = 0.8
29.55s
DCBr
0
5
10
15
[0,5) [5,10) [10,15) [15,20) [20,25) [25,30) [30,35) [35,40) [40,45) [45,50) [50,55) [55,60) [60,65) [65,70) [70,75) [75,80) [80,85) [85,90) [90,95) [95,100) [100,105) [105,110) [110,115) [125,130) [135,140)
Dive duration intervals (s)
c
n = 1725 n = 1076 n = 1535 n = 1155 n = 1913 n = 1081 n = 1115 n = 398 n = 329 n = 135 n = 107 n = 39 n = 16 n = 4 n = 8 n = 2
m = 0.3 m = 1 m = 1.5 m = 1.8 m = 2.1 m = 2.1 m = 2.1 m = 1.9 m = 1.9 m = 1.8 m = 1.9 m = 1.9 m = 1.5 m = 1.6 m = 1.6 m = 0.8
25.06s
DCAr
0
5
10
15
[0,5) [5,10) [10,15) [15,20) [20,25) [25,30) [30,35) [35,40) [40,45) [45,50) [50,55) [55,60) [60,65) [65,70) [70,75) [80,85)
Dive duration intervals (s)


d
n = 347 n = 239 n = 446 n = 363 n = 762 n = 549 n = 810 n = 451 n = 568 n = 275 n = 282 n = 136 n = 129 n = 70 n = 79 n = 33 n = 42 n = 20 n = 16 n = 12 n = 7 n = 2 n = 1 n = 1 n = 2
m = 0.4 m = 0.8 m = 1.4 m = 1.6 m = 1.8 m = 2 m = 1.8 m = 1.7 m = 1.8 m = 1.6 m = 1.5 m = 1.4 m = 1.3 m = 1.3 m = 1.4 m = 1 m = 1.3 m = 1.1 m = 1.6 m = 0.9 m = 0.5 m = 0.4 m = 0.5 m = 0.4 m = 0.5
26.57s
DCAr
0
5
10
15
[0,5) [5,10) [10,15) [15,20) [20,25) [25,30) [30,35) [35,40) [40,45) [45,50) [50,55) [55,60) [60,65) [65,70) [70,75) [75,80) [80,85) [85,90) [90,95) [95,100) [100,105) [105,110) [110,115) [125,130) [135,140)
Dive duration intervals (s)
e
n = 240 n = 356 n = 891 n = 1151 n = 2197 n = 1607 n = 2493 n = 1507 n = 1769 n = 803 n = 749 n = 278 n = 201 n = 55 n = 33 n = 13 n = 9 n = 2 n = 1
m = 0.5 m = 0.9 m = 1.5 m = 2 m = 2.3 m = 2.3 m = 2.2 m = 2.2 m = 2.1 m = 2.1 m = 2 m = 2 m = 1.9 m = 1.9 m = 1.8 m = 2.6 m = 1.8 m = 8.3 m = 10.8
23.32s
DCBr
0
5
10
15
[0,5) [5,10) [10,15) [15,20) [20,25) [25,30) [30,35) [35,40) [40,45) [45,50) [50,55) [55,60) [60,65) [65,70) [70,75) [75,80) [80,85) [85,90) [130,135)
Dive duration intervals (s)
f
n = 60 n = 62 n = 222 n = 287 n = 705 n = 723 n = 1511 n = 1229 n = 1852 n = 1063 n = 1236 n = 599 n = 596 n = 317 n = 329 n = 158 n = 167 n = 78 n = 73 n = 34 n = 25 n = 16 n = 13 n = 4 n = 3 n = 2
m = 0.4 m = 0.8 m = 1.2 m = 1.7 m = 2 m = 2.1 m = 2 m = 1.9 m = 1.9 m = 1.9 m = 1.8 m = 1.8 m = 1.8 m = 1.7 m = 1.7 m = 1.5 m = 1.8 m = 1.6 m = 1.4 m = 1.6 m = 1.3 m = 1.2 m = 0.9 m = 1.3 m = 0.7 m = 1
24.47s
DCBr
0
5
10
15
[0,5) [5,10) [10,15) [15,20) [20,25) [25,30) [30,35) [35,40) [40,45) [45,50) [50,55) [55,60) [60,65) [65,70) [70,75) [75,80) [80,85) [85,90) [90,95) [95,100) [100,105) [105,110) [110,115) [115,120) [120,125) [130,135)
Dive duration intervals (s)

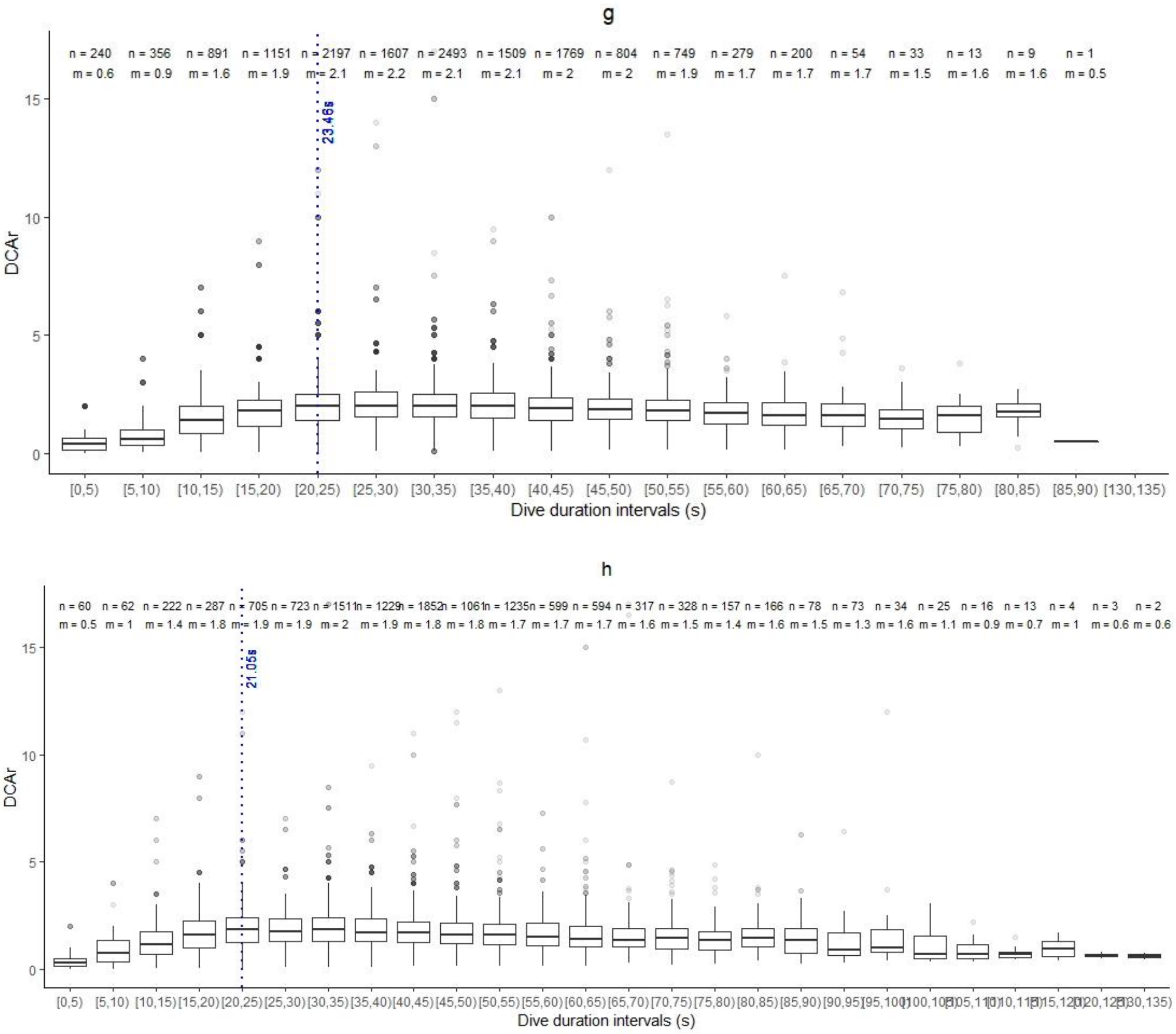


Fig. 13: The effect on dive cycle ratios on dive duration, for DCBr (pre-dive surface duration based dive cycle ratio) and DCAr (post-dive surface duration based dive cycle ratio) separated by sex and dive types NBD (No bottom duration dive) and WBD (With bottom duration dive) - see Table S9. Boxplots are shown for for NBD dives: A) Female DCBr, B) Male DCBr, C) Female DCAr, and D) Male DCAr; and for WBD dives: E) Female DCBr, F) Male DCBr, G) Female DCAr, and H) Male DCAr. n= number of observations and m=mean value. Blue stippled line is the break point found by best fitted piecewise linear regression, true value given by the line (a bit important as some are grouped in categories that they are borderline to cross).

There was no significant difference between the sexes within dive type. Interestingly, however, the peak ratio seemed to be recorded more often in later dive durations in NBD dives than in WBD dives for both males and females (DCBr: Females NBD 28.99 (28.92, 29.97), females WBD 23.32 (21.66, 24.98); Males NBD 29.55 (28.52, 30.58), Males WBD 24.47 (23.08, 25.86); The same result was found in males DCAr.), by several seconds delay and no overlap of confidence intervals.

In Fig. 14 the median of dive lengths (see Methods) were fitted alongside the point in dive duration that returned the peak ratio (Tables 7a & c) based on the piecewise regression; Shags adjusted closer to the presumed optimum ratio in NBD dives than in WBD dives, in both male and female individuals. In WBD dives, males and females both exceeded the optimum ratio (Fig. 14a), whilst in NBD dives males dived very close to the optimum (in fact, in DCBr NBD dives, males peak ratio and median dive durations were estimated to the same second), while females had a clear undershooting. This was true for both DCBr and DCAr. Note the almost bi-modal distribution of female dive duration distributions in NBD dives, with a strong decrease in number of observations straight after the breakpoint, compared to the males more normally distribution of dives around the median.

Table 7: Median dive duration (a), and dive duration of peak and ratio for (b) estimated from grouped intervals of dive duration and (c) estimated through piecewise linear regression.

(a) Dive duration	**Female NBD**	**Male NBD**	**Female WBD**	**Male WBD**
Median	18s	30s	30s	42s

(b) DCBr	**Female NBD**	**Male NBD**	**Female WBD**	**Male WBD**
Peak dive duration intervals	25-40s	25-30s	20-35s	25-30s
Ratio	2.6	2.7	2.8	2.9
DCAr				
Peak dive duration intervals	25-30s	20-35s	25-40s	20-40s
Ratio	2.4	2.4	2.4	2.5

(c) DCBr	**Female NBD**	**Male NBD**	**Female WBD**	**Male WBD**
Peak dive duration intervals	28.99 (28.92, 29.97)	29.55 (28.52, 30.58)	23.32 (21.66, 24.98)	24.47 (23.08, 25.86)
DCAr				
Peak dive duration intervals	25.08 (20.94, 29.22)	26.57 (23.38, 29.76)	23.46 (22.08, 24.84)	21.05 (19.50, 22.60)

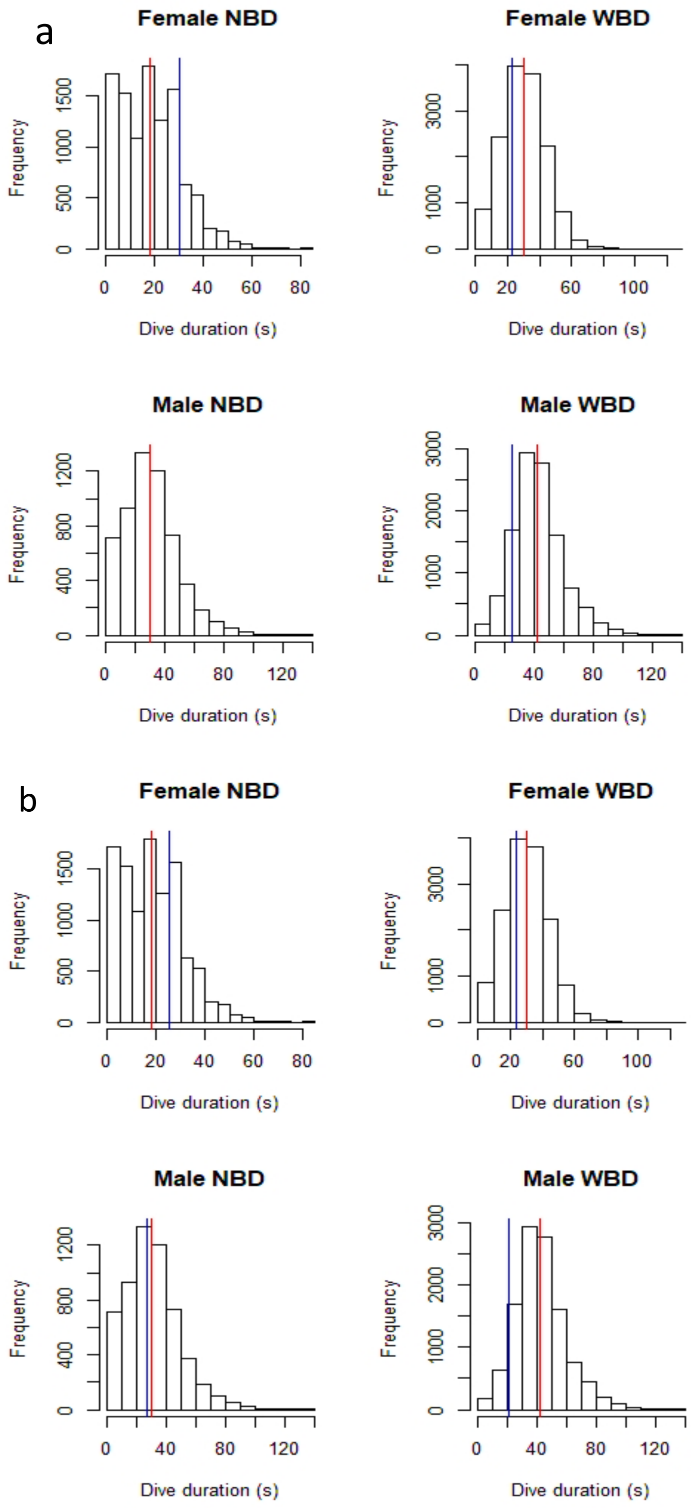


Fig 14: The dive durations (s) separated between sexes and dive types, with peak ratio (blue vertical line) from the piecewise linear regression (Table 7c) and median (red vertical line) of dive duration for the dive type (Table 7a) indicated, for (a) DCB and (b) DCA.

Dive cycles were on average shorter for female individuals than for males (See Table 8, Fig. 15a-b), but increased equally in length for the two sexes when switching from NBD dives to WBD dives (i.e. no interaction). Thus, there was definitely a difference between the sexes, but the increased effort in hunts are of similar magnitude, despite the differences in body mass. The sex difference was expected, as both surface durations and dive durations increase with sex and body mass (See Section 1, Table 2 and Table 3).

Dive to surface duration ratios show no direct variation due to sex (Table 8; Fig. 15a-b). There was however, a positive effect on ratio from dive type, and an interaction between dive type and sex, affirming that the two sexes choose different NBD/ WBD proportions, which again may be due to the difference in bout length (Table 3). WBD dives had somewhat greater dive ratios (Table 8, Fig. 15a & b) than NBD dives (i.e. WBD had relatively shorter surface durations for the same dive duration), and there was an interaction between dive type and sex (i.e. the increase in dive ratio for WBD dives was larger for females than males, Table 8). This again may be due to sex difference in body mass and/or bout length affecting surface times (Section 2B), and linked to the sex differences in travel durations and bottom durations resulting in different dive durations (Section 1A.1).

Table 8: The effect on DCB (pre-dive duration-based dive cycle), DCA (post-dive duration-based dive cycle), DCBr (pre-dive duration based dive cycle ratio), DCAr (post-dive duration based dive cycle ratio) of dive duration, separated by sex for no bottom duration (NBD) and with bottom duration (WBD) dive types. Mixed effect models included identity, location, year and dive date as random effects, which are given as proportions of total variation explained. Fixed effects are given as effect sizes (for non-standardized values) with 95% CIs. Bold numbers for significant values, except in intercepts.

The effect of Sex and dive type on DCB and DCA, DCBr aand DCAr

	DCB	DCA	DCBr	DCAr
Intercept	101.59 (83.56, 118.56)	99.06 (81.19, 117.67)	1.47 (1.24, 1.70)	1.44 (1.21, 1.66)
Sex	**-24.22 (-34.06, -14.50)**	**-23.63 (-33.39, -13.65)**	-8.3e-3 (-0.12, 0.11)	0.02 (-0.11, 0.13)
Dive type	**9.93 (9.22, 10.63)**	**12.32 (11.64, 13.10)**	**0.11 (0.02, 0.19)**	**0.11 (0.08, 0.18)**
Interaction	-	-	**0.19 (0.14, 0.24)**	**0.13 (0.08, 0.18)**
ID	0.24	0.23	0.04	0.04
Location	0.10	0.11	0.03	0.03
Year	0.01	0.01	0.00	0.00
Dive date	0.01	0.01	0.00	0.00
Residual	0.63	0.65	0.93	0.93

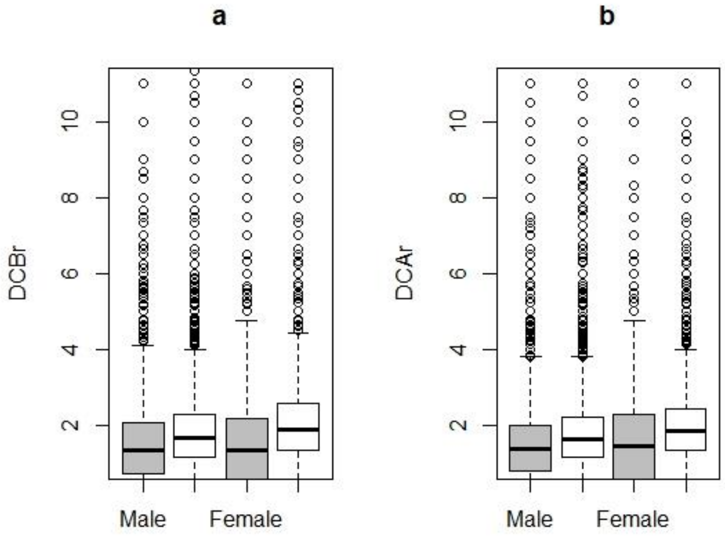


Fig 15: The effects of dive type (no bottom duration NBD [grey] versus with bottom duration WBD [white]) and sex on a) DCBr (pre-dive duration-based dive cycle ratio) and b) DCAr (post-dive duration-based dive cycle ratio), - see Table S9. Mean values are indicated with black bars, and boxes for the interquartile values, error bars represent standard error, and outliers with all raw data included.

It is important to note that in the dive cycle we only assume an effect of dive duration on *one* of the two surface durations. This may be problematic, considering that it overlooks a part of the total cycle tied to a dive (both pre and post dive surface duration), and further, because in the analysis on DCB the effect of dive duration on its own pre- dive surface duration is being tested. Thus, the order of effects needs to be clarified (Section 2D below) to see how the effect of a dives post-dive surface duration is simply tied to the previous dive duration, or whether also the pre-dive surface duration affects the final resting period.

2D: Path analysis for surface and dive sequences

Lastly, the effect of dive duration on post dive surface duration (i.e. was there a recovery effect after longer dives?), the effect of pre-dive surface duration on the subsequent post-dive surface duration, both directly and indirectly through its possible effect on dive duration (i.e. is there anticipatory O_2 storage prior to longer dives?) was analysed. Many of the analyses above have included both pre-dive and post-dive surface times for comparison, because we were unsure which one was the more important. Here we employ path analysis to investigate this issue (see Methods).

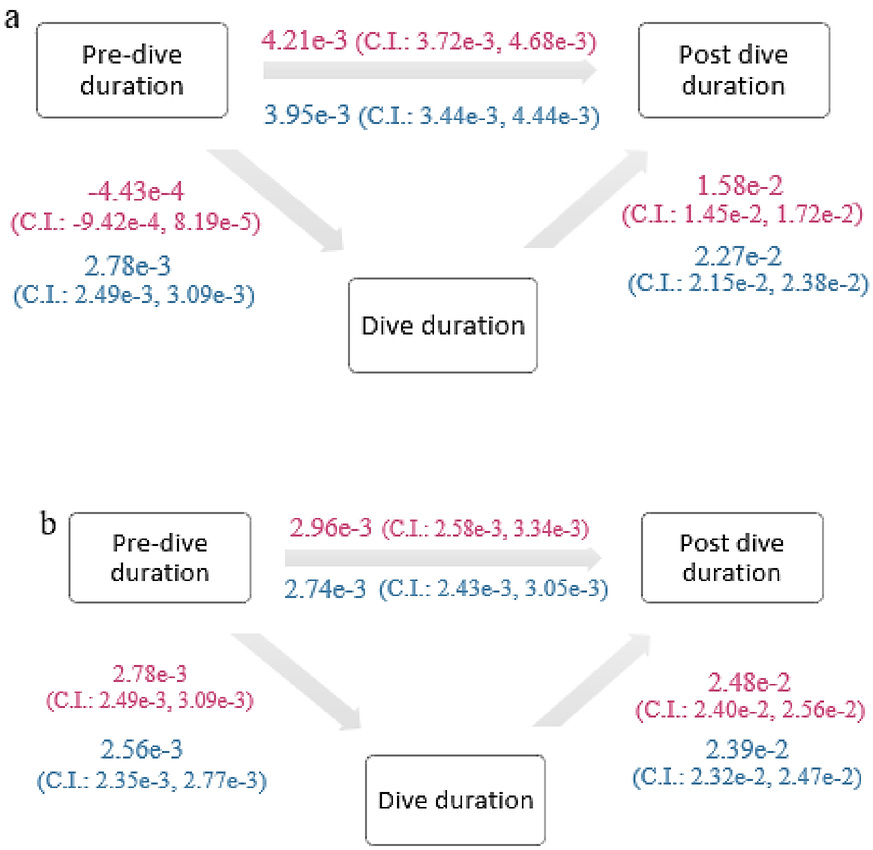


Fig. 16: Path diagram for the direction of effects within a dive cycle with log-transformed response variables, for a) NBD dives and b) WBD dives, with mean values and 95% Cis (female [red]; male [blue]). See Table S10a & b for values in plot.

There was no effect of female pre-dive duration on dive duration (-4.43e-4 (C.I.: -9.42e-4, 8.19e-5)). However, as pre-dive duration increased (Table S10a), so did the dive duration by 2.78e-3 (C.I.: 2.49e-3, 3.09e-3) in female WBD dives, 2.78e-3 (C.I.: 2.49e-3, 3.09e-3) in male NBD dives and 2.56e-3 (C.I.: 2.35e-3, 2.77e-3) in males WBD dives, indicating a direct effect of surface duration on the subsequent dive duration (Table S10a-b, Fig. 16). Interestingly, the effect of pre-dive surface duration was strong in females WBD dives, but non-significant in NBD dives, whilst equally high for males NBD and WBD dives, suggesting that pre-dive duration activity is different before a WBD dive than an NBD dive in females, but equal in males.

Further, an increased dive duration increased the length of the post dive duration (1.58e-2 (C.I.: 1.45e-2, 1.72e-2) for female NBD dives, 2.48e-2 (C.I.: 2.40e-2, 2.56e-2) for female WBD dives, 2.27e-2 (C.I.: 2.15e-2, 2.38e-2) for male NBD dives and 2.39e-2 (C.I.: 2.32e-2, 2.47e-2) for male WBD dives; See Table S10b), indicating that there was a certain penalty of an increased dive duration (i.e. there must be a trade-off between pursuing prey and minimizing post dive surface duration). The effect of an increased pre-dive duration on post dive duration was positive (by 4.21e-3 (C.I.: 3.72e-3, 4.68e-3) for females NBD dives, 2.96e-3 (C.I.: 2.58e-3, 3.34e-3) for females WBD dives, 3.95e-3 (C.I.: 3.44e-3, 4.44e-3) for male NBD dives and 2.74e-3 (C.I.: 2.43e-3, 3.05e-3) for males WBD dives), with a slightly smaller effect size than by dive duration though significant for both sexes and dive types. In other words, as dive duration increased, post dive duration increased as a response. As pre dive duration increased, so did dive duration leading to a further increase in post dive duration. However, pre- dive surface duration had an additional, direct effect on post-dive duration (Table S10b), with similar magnitude as the effect of pre-dive duration on dive duration (Table S10a). Interestingly, there was no effect of pre-dive duration on dive duration in female NBD dives, but a strong effect in WBD dives, suggesting difference in preparation strategy before a dive, possibly in loading of additional O_2 into body stores.

Lastly, it should be noted that there were hardly any difference between NBD and WBD dives in males dive duration effect on post-dive surface duration (Table S10b). The effect of pre-dive surface duration was stronger in NBD dives than in WBD dives in both sexes, suggesting that an increase in pre-dive duration before an NBD dive had a much larger effect than in WBD dives, possibly because the effect would be divided into fewer seconds (as NBD dives in general are shorter than WBD dives, see Table 3).

The path analysis reveals a clear direction of effects, where a more complex sequence of events determines the final length of post dive surface duration. The path analysis sheds light on the issue of dive cycles either including pre- or post dive surface durations (Section 2A.1), but never both, meaning that the whole sequence of events that highly affect each other is not taken in to account. Thus, the results may be an underestimation of effects on post-dive surface durations.

Discussion:

Investigating the main determinants of European shags foraging strategies:

The descriptive analysis here of sex differences, dive types, body mass, speed and seasonal changes provided a secure platform that was necessary for any interpretation of the findings from testing the MVT in the second half of the Results. Walton et. al. (1998) carried out a physiological assessment of the MVT largely based on assumptions that they did not really have the data to test themselves. The SeaPop dataset from the Sklinna population provides a way of answering many of these outstanding issues, as well as some new questions that presented themselves during these analyses. Firstly, our dataset was large enough to split into subsets separating the sexes and the dive types, leading to a much more detailed insight when considering optimal foraging (i.e. being able to separate out apparent non-foraging dives, and splitting by sex to assess independently the effects of body mass). The separation of the sexes was useful due to dimorphism in body mass in shags, and the prediction that body mass would lead to a direct change on the peak ratio measured. Importantly, we tested the relationship between dive depth and dive duration for the assumption of linearity, but in our data this was not the case for the WBD presumed hunting dives. This problem was solved by simply applying travel duration instead of depth when testing the MVT.

Further, Walton *et al.* (1998) assumed that shags utilized a 'switch metabolism' involving use of air-sac O_2 and then blood O_2 stores (see Huston and Carbone 1996). We found support for this in the results here, with only one peak in the effect of travel duration on bottom duration and on dive cycle duration. The metabolic pathway here is essential for the assumption of a kinked O_2 up-take rate (see Fig.2, Introduction) and thus the predictions of a refined version of the MVT. The MVT predicts that travel duration and gain should be tightly bound together in a particular relationship (see Introduction), but this may not always be apparent in field data like ours of shags if other trade-offs are in play. Thus, investigating the diving strategies of the sexes in different situations (i.e. dive types) was key to interpreting statistical tests of the theorem in foraging dives of shags. The result was an intricate analysis of the MVT predictions in the context of a complex ecology of a diving bird involving ideas from many areas of behaviour and physiology, which was necessarily incomplete due to the lack of time in a masters project for what turned out to be a very complex set of results.

Separating foraging from non-foraging behaviour:

There was a strong effect of dive type - no bottom duration (NBD) versus with bottom duration (WBD) - on all tested dive parameters except surface durations (Subsection 1A, Table 4). The general effect strongly suggests that the data contain two types of dives, perhaps equating to ‘sampling’ dives where no prey was caught (NBD) versus ‘hunting’ dives where prey was actively pursued and perhaps caught (WBD). However, questions have been raised as to how hunting versus information sampling dives were categorised. It seems reasonable to assume that there will be some dives where no prey was located (i.e. during NBD dives). Birds have very good eye sight (Meyer 1977), the Nordic water is clear and the prey stay in shoals, so there seems to be no reason for a shag to conduct lengthy horizontal underwater pursuits if they haven’t visually located prey from a distance, unless during NBD dives they were employing a hunting tactic of scaring prey out of its hiding place. Further, shags may have had a maximum limit (i.e. in available in O_2) of a few minutes per dive and a thermal loss higher than most diving animals (including other avian divers) due to their semi-wettable plumage (Grémillet 2005), so long dives involving a low chance of successful gain should have been avoided (see below).

As expected, WBD dives had greater maximum depths, although descending and ascending to same depths as in NBD dives took a shorter amount of time for WBD dives. We concluded, however, that the increase in travel speeds in WBD dives compared to NBD dives probably reflects the greater swimming speeds while actively pursuing prey (i.e. during bottom time) that was reflected in greater speeds at the end of descents and at the start of ascents. As speed increases so does hydrodynamic drag (Squire, 1957), and thus energetic, physiological time and/or energy costs should increase (Williams, 1999). The increased presumed swimming cost in WBD dives agrees with the suggestion that WBD dives are hunts that last over longer durations than NBD dives. This is not to say that prey cannot be caught in an NBD dive (i.e. while travelling vertically down and back up again), but as a general rule these dives do not appear to involve prey capture opportunities. One way to test the dive type hypothesis directly would be to additionally fit a thermometer in the stomach of the shag to detect cold prey ingestion (see Future Research below).

How variation in body mass led to sex specific foraging strategies:

There was a strong effect of sex (male versus female) on all dive parameters throughout much of the analyses. This might reflect sex differences in body mass or inherent differences in male versus female physiologies and foraging behaviour. However, sex and body mass were hard to separate statistically, and there were significant interactions between dive type and sex, body mass and dive order, body mass and dive type, plus dive order and sex, all of which further complicated any interpretation. Hence, we chose to explore the effects such as body mass within each sex and dive type separately, and then to compare the trends to see if they matched those expected from the body mass differences alone. This led to one of the most important findings, establishing that females and males within the same body size range seemed to choose the same strategy in terms of dive depth, duration and number of dives per bout. A separate analysis emphasized that body mass effect and sex effects were completely overlapping when comparing the mean mass difference between sexes (see Appendix, Table S5). Thus, when correcting for body mass, all individuals of both sexes appeared behave the same way in all dive parameters except perhaps for in surface durations where there were interestingly no effects of body mass (see below).

The body mass difference between the sexes is probably the result of sexual selection for large males, with females being optimally sized for the species ecological niche (Payne 1984). There are two non-mutually exclusive explanations for this selection. Firstly, there could be a selection to reduce competition between the sexes (Selander 1966, Aulén & Lundberg 1991, Radford & du Plessis 2004), with females and males essentially foraging in different vertical areas in the water column, leaving a greater prey abundancy for each of the sexes, and possibly even affecting the geographical locations males versus female choose to forage in. There was, however, no obvious sign of the sexes choosing different patch locations in our data, although a more complete analysis still needs to be carried out (see Further Research below). In addition, the sexes showed considerable overlap in dive depth and duration, even if males in general choose somewhat deeper dive depths. The other explanation is that there should be an increased cost of foraging for larger individuals. Such a cost could be based on the increased hydrodynamic drag and buoyancy cost for larger bodies in water (Squire 1957). The largest energy and thus O_2 drain for divers is not the gravity as it is for terrestrial animals, but the sheer resistance in water due to density, viscosity and movement which decreases with depth, otherwise known as hydrodynamic drag (Squire 1957; Williams 1999). Thus, large males may need to dive deeper to avoid the costs of locomotion in shallow waters. Conveniently, larger bodies are also capable of larger O_2 stores and muscle capacity, facilitating such diving strategies.

Sex specific foraging strategies unrelated to body mass:

The sex difference in surface durations remains a riddle. None of the tested explanatory variables had a convincing effect on these resting periods according to sex or dive type. The mean surface duration for males lasted more than 10 seconds longer than for females, but body mass had no effect, and dive order only affected surface durations positively in male NBD dives (but with a decelerating effect due to the interaction between dive order and body mass), and overall there were no difference in surface durations between the dive types. Further, the only random variable that explained a substantial amount of the variance in surface durations was individual identity, suggesting some unidentified difference between individuals in their diving behavior within bouts. Temperature, weather and contrasting foraging strategies are reasonable areas to pursuit for answers (see Future Research below).

Male NBD dives should have been more costly due to their increased depth. Thus, it may be favorable for males to avoid excessively long NBD dives, and to compensate for the lack of information by waiting a little longer on the surface in order to let prey return, result in an alternative strategy for males compared to females. This hypothesis was supported by the fact that male birds, in general, had a smaller proportion of NBD dives to WBD dives, compared to females. Both information sampling and "waiting out" prey are reasonable strategies, and although both are expected in each of the sexes, it may well be that longer pauses were used with a higher frequency by males. Additionally, prey in deeper depths may need more time after hunts for the shag to regain the element of surprise, an element that may be critical for large males who must swim far to reach its prey. Some effect of body mass was therefore still have been expected, but none was found, and so the increased surface duration of males was the first sex-specific behaviour here that could not be explained by the body mass difference.

Interestingly, Enstipp *et al.* (2001) showed that surface duration increased with decreased motivation for diving, when testing surface duration against prey type. It is not expected that prey type is different in an open marine system for shags foraging in overlapping depths, but there may be a change in motivation for pursuing provision when the stomach content has increased. If there is a difference in the parental effort of shags, a male shag may be less motivated to keep hunting when its own needs are beyond satisfied. According to Wright & Cuthill (1990) there could be sex differences in parental effort when brood demand is low (e.g. when chicks are at a young age). Female shags will have recently put in a large effort in laying the eggs, brooding and (possibly more than the males) invested in provisioning younger chicks. Thus, they might have a higher motivation for further investment if their future prospects. With approximately 35 days old chicks, the brood demand during this study may still be relatively low, but rapidly increasing, and synchronization in food delivery between parents may not be entirely stabilized, again suggesting why there were no clear effect of nest identity (see above). However, as Wright & Cuthill (1990) explained, there should be no variation in how the shags behave when foraging, just the amount or length of trips taken. Thus, spending more time on the surface within a foraging trip is less likely to be due to a low motivation for parental investment, and more likely to be a way of increasing the chance of success.

The effect of physical forces on body mass in an aquatic system:

Body mass had a greater positive effect on dive behaviour in the lighter individuals (i.e. females) within the sample, perhaps as body mass levelled off at some point for heavier (i.e. male) individuals. The results presented here suggest that larger individuals that achieved higher descent and ascent speeds also chose to go deeper and chose to dive for longer durations before replenishing O_2 stores. Travel descent and ascent speeds increased significantly with body mass, but only for females, perhaps because hydrodynamic- and wave- drag along with buoyancy created a counter-current effect, as they all increase with the increasing volume of a body (Squire 1957). Drag, in theory, increases with increasing depth due to increasing water density, but this is unlikely to have a large effect within the span of our observed dives. Instead, drag and buoyancy effects should be largest closest to the surface and decrease with depth, due to the turbulence of wave induced drag (Squire, 1957). This implies that the larger shags may have to go deeper to avoid the increased cost, but that at some point further increased depth did not make a large difference in cost of movement- and so, there would be no use for even larger individuals to further increase depth. Thus, medium to large individuals (i.e. large females, and males in general) may seek the same depths, where prey is present but buoyancy and drag is decreased.

The developing foraging patterns throughout a diving bout:

Females performed relatively more NBD dives per bout than males (female: 45%, male: 34%). Females also performed a larger number of dives per bout, but males compensated for this with longer dives within each bout. This suggests that females hunted at shallow depths with lower prey density resulting in more NBD dives without bottom duration (i.e. sampling dives), or that males more often chose to pursue prey that for females were judged to be unobtainable. For both sexes, the proportion of NBD dives increased with the bout length, and thus females may have had a larger proportion of NBD dives simply due to the longer bouts. Further, the chance of a dive being an NBD dive increased with dive order, which suggests that longer bouts may have tended to end with high frequency of NBD dives as a sign of a decreasing rate of prey encounter following diminishing returns, causing birds to end a bout, and possibly travel to another location. This is likely, considering that shags often visit multiple foraging locations in one foraging trip, where locations visited early in a trip may be connected to self-feeding behaviour, possibly on larger prey that prefer deeper depths (see future research). Whether a location is used for self-feeding or chick provisioning may be testable. Self-feeding should happen early in a trip (i.e. for proper digestion of larger prey that may be regurgitated back to chicks by accident), and should contain few dives/bouts (short in-location time), with high rate of WBD dives (see Future analysis).

Further, it is implied that in optimal foraging behaviour the shag should leave a patch if the rate of gain becomes lower than average and move to a patch with higher rate of gain- to increase efficiency in foraging. If the frequency of NBD dives becomes too high, this may be the que to leave the foraging patch in search for a new and better option, or even give up and return to the nest. It is worth noticing that the amount of food a shag brings back to its chicks is of significant weight compared to own body mass (Grémillet *et al.* 1996), and this load would be additional to the self-fed prey mass. Thus, a shag may be slowed down by the increased weight, and possibly an increased metabolic rate due to the onset of digestion (Wanless *et al.* 1993), as well as cost of transport (Williams 1999).

An alternative explanation, that bouts were ended not because of a lack of prey but because individuals reached a physiological limit of successive dives (e.g. emptying of O_2-stores, lactate production, etc., as described for forced dives by Scholander, 1940), was rejected as dive duration distributions for each individual as well as within sexes were normally distributed, rather than truncated at some physiological maximum value. However, in the case of thermal limits such an abrupt endpoint may not be as visible, as it should be highly dependent on dive order and work load within a dive (i.e. heat production) and the previous dives and the cold of ingested prey (plus load size and time since ingestion), as well as depth and surface to volume ratio of the body (Enstipp *et al.* 2005). Whether the true determinant was a matter of energetic fatigue or thermal complications, a cost-benefit trade-off such as diminishing returns of prey encounter, or simply the amount of time it takes to catch a fish in a given location is currently unclear.

Dive order (i.e. the number a dive had in consecutive series of dives in a bout) had a surprisingly large effect on the behaviour within each dive for males. The numerous negative interactions seen between dive order and body mass in males are interesting and suggests that there is a relationship between the behaviour of males and their size, in relation to the order of a dive. Possibly, as WBD dives became deeper with increasing order, body mass affected how much deeper the shag went. This again may be connected to drag and buoyancy issues levelling off with increased depth. Both body mass and dive order had positive effects on depth, but there may be a limit to depth -either due to the depth of location or simply the depth necessary to overcome to reach zero buoyancy. Further, large individuals are noted to keep bout lengths shorter than the smaller individuals, and thus the negative interaction between order and body mass slows down the depth of large individuals in longer bouts. Females performed more than 30% more consecutive dives per bout than males, and so maybe the effect of body mass became a more important factor during such lengthy dive bouts. Both body mass and dive order had large effects separately in females, but when put together dive order often lost much of its effects to body mass, suggesting that the effects of dive order might be due to similar biological effects as dive order.

The only thing that seems certain is that the sex difference in shag foraging dive strategies appear to be tied to a range of body masses leading to an equally continuous responding range in bout lengths, depths and dive durations strategies. Finding that any sex differences are merely an effect of body mass differences creates a foundation to explore these data in more detail in the future. The division here into the two sexes was a simple and practical solution to somewhat correct for the body mass and/or dive order difference between males and females while exploring and comparing the effects of body mass within the two sexes. As the dataset was divided further, between the types of dives the numerous interactions within explanatory variables (see above) was avoided.

Female WBD dives proved to be slightly shallower with increasing order, while the effect of dive order was positive in males, suggesting a convergence in behaviour over lengthy bouts for the two sexes. Female WBD dives could have become shorter and shallower perhaps due to energetic fatigue and low body temperature as a result of long bouts, or simply reflecting the fact that the birds had already obtained a certain biomass of prey in the bout, and so were satisfied searching for smaller prey in shallower dives to complete a load worth delivering back to the nest. The slightly negative effect of order on females WBD dive maximum depth is less likely to be a sign of thermal or energetic fatigue, as the dives did not decrease in duration during a bout. Rather, diving strategies seemed to reflect differences in body mass; a small body can more easily stay in shallow waters with a smaller cost of hydrodynamic drag and buoyancy (see above). Increasing prey load in the stomach, the following weight and increased metabolic demand may also be a supplementary reason for dives to become shorter towards the end of a bout, though probably not enough to explain the shallower movements in itself considering that males NBD dives seem to increase in depth and duration.

A possible explanation to the opposite effect of dive order in WBD dives for males and females could be either: a difference in hunting strategies between the sexes (e.g. females chasing prey to shallower areas or possibly closer to the surface/into kelp forests, whilst males chased prey into greater depths), or alternatively, this could simply reflect the escape strategy of the prey, based on their size, the depth they are in and the depth dependent hiding opportunity (e.g. in kelp forests) at the given depth. The negative effect in females were very small, and implying a limitation in how shallow prey are able to move. In the opposite end, there may be less of a limitation to how deep prey were willing to go when hunted in deeper areas. Thus a positive order effect is apparent for shags who choose to hunt in the deep (such as our finding in male shags) while no change or a slightly negative effect on depth were visible in shags choosing shallow areas with little change in dive durations (i.e. female shags).

Interestingly, WBD and NBD dives became more and more similar in depth and duration as dive number increased. For example, in bouts of 100 dives, there would not be any difference between male NBD and WBD dives in depth nor duration, and although this bout length was far above the mean, it cannot be seen as uncommon (>20 observed bouts). The increasing dive duration and depth of NBD dives was not very intuitive. There could be an increased investment in sampling towards the end of a bout (i.e. when most of the available prey have been recently caught or scared off), if the shag wants to be absolutely sure it is not missing out on an opportunity before ending a bout. If the shag knows that rest and rewarming is close, investing more (e.g. by increasing blood lactate) in the sampling may not necessarily increase the immediate costs in terms of surface time, if they anticipate taking a longer break in the near future. Alternatively, the reason NBD and WBD dive depths and durations converged towards the end of bouts could simply be that as the local environment becomes more predictable (i.e. having more information about a patch after a lengthy bout than before), the depth where prey is located and the duration it should take to get there or leave becomes more consistent across dives whether prey are located or not, thus the two dive types converge to the depth that is most profitable in that patch. More analyses of location-specific convergences of the dive parameters for the two types of dive would perhaps be needed to test these ideas.

An interesting question is whether the shallow diving individuals and the deep divers capture the same sized prey. If they do not, this may explain why males can have so many fewer dives at deeper depths, although any such possibly larger prey captured must be fit for a 35d old chick, or in a size range where it can be pre-digested and broken up sufficiently by the parents in the short time before delivery to the chicks. Even if males and females go for the same sized prey, there is still a possibility of self-feeding (Ydenberg 1994). Shags can visit several locations per foraging trip, and some locations or bouts may indeed involve self-feeding on larger prey, where the foraging strategy changes (see below concerning further analyses of these data).

Variation in hunting strategies for provisioning parental European shags:

Another issue to address on hunting strategies is the question of whether shags catch single or multiple prey in one dive. If they catch multiple prey, the increased bottom duration may reflect increased prey intake per dive. If they only catch a single prey per dive, an increased bottom duration reflects the opposite and a longer chase time per prey, although this could be worth it for a larger prey item. An increased success rate or size of prey (e.g. at those deeper hunter depths) may explain why males can have less WBD dives in a bout than females, but still deliver their share of food to the chicks and gaining enough energy for them self. The trade-off between number of dives and dive duration may therefore be an interesting issue leading to changes in biomass delivery to the nest. This is not entirely unlikely since early in breeding (i.e. chicks approximately 35 days old) prey sizes may be limited to those the chick can ingest and parent shags mainly feed on smaller group 0 to group 3 saithe (*Pollachius Virens*), cod (*Gadus morhua*) and sandeel (*Ammodytidae* spp.) and other, small items of prey (Lorentsen and Hillerøy 2012). One way to test this could be to take the stomach temperature during a dive (see above and Future Research below) and see if the shags abort or continue dives after gastrointestinal temperature decreases.

One striking result was how much variation in these data was explained by individual identity, which was substantially more of the random noise in WBD dives than in NBD dives. This suggests that individuals behaved similarly in NBD dives, but that any individual variation in behaviour (e.g. individual or mass-specific swimming or hunting styles) was revealed during WBD dives. This finding supports the idea that WBD dives were active prey hunts, whereas NBD dives were simply sampling dives with less opportunity for individual variation and innovation.

Another interesting result was the substantial effect that location had on bout lengths and other dive parameters, perhaps indicating chick-feeding versus self-feeding patches (Ydenberg 1994; see below for discussion of future analyses that was not possible in the timeframe of this project). Location also proved an important factor for dive durations and depths, which may reflect the different qualities of the patch bathymetry, or simply the size of prey, abundancy and vertical distribution of prey. All locations appeared to be attended by both sexes, but deeper investigation into location-specific effects of sex and body mass, and possible location preferences according to sex, body mass or individual identity are now needed.

Variation in foraging ecology for an avian diver:

Interestingly, nest ID (i.e. individuals belonging to the same nest or pair) was tested as an additional random effect, but it rarely explained more than 0.0002% of the variation in dive parameters, suggesting that conditions related to the nest, brood or pair explained fairly little of the behaviour of individuals. We expected to see at least some effect due to brood demand that could be similar for the parents of shared nests, as the data from both parents were taken in the same period (See Methods). However, as Wright *et al.* (1998) discussed, brood demand should not affect the optimum central place foraging strategy, but that parents should maximize the net energy gain in any foraging trip, and rather distribute the gain differently between the brood and themselves. For simplicity, nest ID was therefore removed from all models (see Methods).

Year had only a minor effect on the data. However, correcting for year is generally recommended in studies of marine birds, due to the frequency of year-to-year variation in marine systems (See introduction) such as El Niño years which appeared in 2 years within dataset: 2015-2016 (Henley *et al.* 2017). Dive date was included as a random effect, even though it was nested in year, because the two parameters provided different assessments of variance; in dive date the day-to-day changes in the environment due to weather and season were accounted for. In year there may have been less variation, but critical differences could be detected, as effects that were due to more general long-term effect (climate and weather).

The effect of season was often significantly negative for male dive parameters, but a strong positive effect in the same parameters for females. Interestingly, the sexes differed most in their dive behaviour early within each breeding season, and gradually converged to end of the season with quite similar dive parameters. Body mass and dive order appeared to be the main explanations for the sex difference in shags diving behavior, and so the seasonal effects may be due to change in body mass, where females in general were heavier towards the end of the season, and/ or males were smaller. Whether there are any seasonal changes to body mass within or between individuals is yet to decide. As an alternative explanation, prey may change in abundancy, or in their vertical habitat during the season. Either way, the difference between the depth and duration of dives became more similar between the sexes with season, challenging the hypothesis of sex-specific strategy to decrease competition (see above).

Testing the Marginal Value Theorem in parent shag foraging dives:

We tested the Marginal Value Theorem (Charnov 1976) to better understand the travel durations and the responding foraging durations of central-place foraging dives by parent European shags. First, the theorem was tested on the dive cycle, similar to the simplistic method described by C. W. Clarke. (Stephens *et al.* 2007) of determining the diminishing return in total dive cycle (dive + surface duration) with increasing dive duration, suggesting a difference in time it takes to replenish respiratory versus blood/tissue O_2-stores. Further, the relationship between dive cycles and dive duration could be used to find the optimal dive duration for a given travel duration. Then the theorem was tested directly on the relationship between travel duration and foraging duration, where we found that the further a shag travelled to a foraging location, the longer it spent foraging in the patch, probably returning a larger load of prey from longer trips than shorter ones.

The optimal dive duration from the diminishing returns, dive cycle-curve was used to extract the predicted bottom duration (see methods). The correlation between observed and predicted bottom duration was used to analyse the optimality between travel duration and corresponding time spent foraging. To strengthen the foundation for the further analysis on dive to surface ratio, we used Houston and Carbone's (2995) method to find evidence that supported the assumed O_2-depletion of respiratory body stores prior to the blood and tissue O_2-stores. This was important to establish, because a peak ratio in dive to surface ratio would not appear due to the difference in time taken for replenishment of O2-stores if they are simultaneously depleted. Further, it gave support to the discussion of diving strategies and the lacking difference in surface duration between dive types (See discussion above).

As a further refinement of the previous marginal value investigations, we applied the sophisticated approach of Walton *et al.*'s (1998), taking the physiological aspect of avian gas-transport into account and looking for a dive to surface peak ratio that would reveal the point of where the diver shifted from respiratory to blood and body tissue O_2-stores. This was determined, firstly by fitting dive duration intervals to the corresponding dive to surface ratio, determining a plateau to which a more precise peak ratio should appear in. Then, a piecewise linear regression was fitted to establish this more precise point, and to compare the slopes before and after the peak ratio, and between the dive types.

Lastly, a path analysis was run, to establish the order of effects for pre-dive duration on post dive duration, directly and indirectly- through the effect of dive duration on post- dive duration. This method was conducted to determine that pre-dive duration had an impact on post dive duration, and that an order effect within an extended dive cycle would be necessary to take into consideration in future analysis. All of these mentioned analysis were interpreted by the basis of the findings from Results, Section 1.

Investigating the physiological adjustment of O2-store size and utilization:

As dive duration increased, total dive cycle (DCB and DCA) durations showed the predicted exponential increase (Stephens *et al.* 2007), suggesting that the birds adjusted surface durations according to the costs of increasing dive durations. These results show that longer dives demand a more profound depletion of hemoglobin and myoglobin-bound O_2, leading to a non-linear increase in surface duration and therefore also total dive cycle durations. The exponential increase indicates the dependence on partial pressure of uptake rate between the tissues and the atmosphere, resulting in a relationship of diminishing returns - see Introduction. All of this was true for pre-dive as well as post-dive durations, and a significant difference was found between the dive types in pre-surface durations, which raised the interesting question of (in the absence of series of NBD or WBD dives) whether dive type was decided before or during each dive.

We know that there were no differences in pre- and post-dive surface durations between the dive types, which was surprising, considering that dive durations in general were much longer in WBD dives than in NBD dives, and further so when seeing that the length of pre-dive duration positively affected the dive duration (in the path analysis, longer pre-dive durations would lead to longer dive durations). The lack of change in surface duration between the dive types may be explained by the experiment of Lasiewski and Calder (1971) of birds ability to decrease their respiratory tract turn-over rate by half, meaning more time and/or effort is invested in preparing for longer dives that are more likely to provide sufficient rewards in terms of prey capture - see Introduction. If our birds indeed increased their O_2 uptake rates, there would not be any difference in surface duration between the dive types, but still a visible increase in dive duration- as we found, leading to a much more efficient use of time while prey is present. In fact, the steeper increase in surface durations connected to NBD dives compared to WBD dives lets dives that last for more than about 50s longer than an NBD dive have the same dive cycle length (see Fig. 9). The path analysis showed that there was a distinct difference between the effect of pre-dive duration on dive duration between the two dive types, indicating such a possible adjustment. Post-dive duration did not increase distinctively with dive type, but this is not really surprising. During post-dive duration (doubling as the pre-dive duration for the subsequent dive, due to the nature of bouts with a consecutive series of dives), an individual must begin to pay any aerobic and anaerobic debt (release CO_2 and metabolize lactate) from the previous dive (Kooyman 1980). If the individual dives again before the full debt is paid, the metabolizing on CO_2 and lactate will continue during the dive, shortening dive duration and accumulating debt further (Kooyman 1980); Thus, accumulation of lactate should always be avoided for divers with multiple consecutive dives in a short amount of time. A more profound dive response (Irving *et al.* 1935, -see Introduction) in WBD dives could arguably be the reason for the increased dive duration, but this is less likely to explain the lack of differences in surface duration between dive types.

Optimality in decision of dive type:

The ability of a bird to increase their uptake rate of O_2 raises an interesting question: when is the dive type decided upon? If the dive type is decided only during a dive (maybe as it closes up on the peak ratio in Figs. 13), the shags should maximize the O_2 loading before every dive, thus being most time efficient. However, if it is decided upon before a dive, pre-dive surface duration could be key in understanding the length of a dive. If the dive type is decided during a dive, shags should always prepare for an optional WBD dive, but abort during the descent if no prey are detected. A strategy of deciding dive type once in a dive can be explained as an adaptation to a stochastic environment where prey locations are unpredictable. The large uncertainty concerning prey encounters in a demanding environment (low temperatures, high thermal conductivity and no vacant O_2) means that shag should evolve an opportunistic foraging strategy (see Introduction). This could arguably be the reason to our findings that male pre-dive surface duration had an equal effect on the dive duration in NBD- dives and WBD dives (See path analysis), meaning that there could be no difference in preparing for the two dives.

Thus, it seems as if males prepare for some maximum dive duration for every dive, whilst females indeed seemed to change their preparation strategy between dive types, shown by the increased pre-dive duration effects on dives duration and post dive duration in the path analysis. It was determined that pre-dive surface duration had a substantially larger effect on dive durations in WBD dives than in NBD dives, meaning that this period of time could be more efficiently used. In fact, the effect of pre-dive duration in females WBD dives were in the same size range as the male effect of pre-dive duration in both NBD and WBD dives, whereas the female NBD dive effect was halved. This implies that although always preparing for WBD dives could be efficient, it may come with a physiological cost when dives are shorter and that in such cases planning the dive before executing it is more favourable. The prediction of cardiac stress being a determining factor (see Introduction) seems plausible for divers with long bouts. The strain on the heart may be worth it if bouts are short (i.e. male bout lengths compared to female bout lengths), because the accumulating coronary hypoxia may not manage to become fatal. And so, if a small individual (i.e. female) assumes that prey is still around after a detection during the last dive, the bird would increase the uptake rate to rapidly be prepared for a proper hunt during the subsequent dive, for example by increasing heart rate and breath cycle frequencies. Shorter WBD dives could reflect the birds grabbing a chance of chasing close prey in an un-planned WBD dive (i.e. that was planned as an NBD dive).

Complimentary to this possibility of cardiac stress costs is the issue of greater thermal regulatory costs for smaller individuals, implying that body mass could be a major driver behind the different strategies. Smaller individuals have longer bouts, and smaller bodies that may have a larger struggle in keeping up their body temperature. A decreased temperature in blood increases the work of the cardiac muscle, due to the higher viscosity of cooled blood, but even more importantly, increased metabolic demand to thermoregulation (i.e. body temperature is kept at homeostasis in the cold environment) may also demand harder work from the heart by high frequency of heart beats (Sun *et al.* 1997). Because their bouts are longer, smaller individuals (i.e. females) may be forced to plan their dive types, preparing only for dives that may return gain, whereas larger individuals (i.e. males) with relatively smaller thermal costs (due to small surface to volume ratio of body, or even simply due to the shorter bouts) may instead plan a maximal dive duration every time, planning less flexibly and deciding once down there between dive types. Also, due to the larger preferred depths in males, the surface is further away, and so NBD 'sampling' dives carry a heavier travel cost and any dive should perhaps have greater potential to become a WBD active 'hunting' dive. The question of whether dives are planned prior to- or during a dive could be resolved out by monitoring heart rates and connecting them to TDR data of dive type and dive duration, to look for relationships between preparation for a dive, the dive type and dive duration (see Future Research below).

In addition to no effect of dive type on pre-dive duration, there was no effect of dive type on post-dive duration either. This is not really surprising, considering that during post-dive duration, an animal must begin to pay any aerobic and anaerobic debt (release CO_2 and metabolize lactate) from the previous dive (Kooyman 1980). If the animal dives again before the full debt is paid, the metabolization of lactate and release of CO_2 will continue during the dive, shortening dive duration and accumulating debt further (Kooyman 1980). Thus, shags in general should avoid any lactate accumulation, as they are dependent on having multiple dives over lengthy bouts with little room for proper breaks (<360 sec in our analysis) between the dives. Therefore, no large change in post-dive surface duration is expected at all, when the alternative of increasing pre-dive work load is an option (i.e. increasing dive duration without increasing surface duration) (Fedak 1988). Further, avoiding penalizing post-dive surface duration is especially important in environments where much sampling may be needed, such as in a stochastic marine environment, with rapidly moving prey and vast distances between the clusters of food (Schreiber and Schreiber 1989). It needs to be noted that when investigating the exponential relationship between the dive cycles and the dive duration, a large amount of extremely short surface durations was found connected to long dive durations. The finding was indeed surprising and should be investigated further (see Future Research below).

Observed change in foraging duration with an increasing travel duration:

Short travel durations had correspondingly short to medium bottom durations, but as the travel became longer, the time spent actively foraging increased to compensate. The increase in bottom duration by travel duration in shorter dives is in line with the MVT (Charnov 1976; Stephens *et al.* 2007) predicting that when an individual has travelled far, it is expected to make up for the time spent travelling by returning more gain than from a short travel. At a certain point, the observed lengths of the travels started to have a decreasing effect on the bottom duration, presumably because there was a maximum dive duration limit that had to be divided between the two activities as a trade-off, overruling the trade-off between prey investment and surface duration.

The non-linear change in bottom duration as a response to increased travel duration was very much as expected, as one of the three assumptions in the MVT states that an individual should maximize its ratio of time between the intake of resources and the time spent (Charnov, 1976). The overall result suggests that there were numerous deviations either side of the optimum that didn't necessarily maximize bottom duration as predicted by the MVT. This is presumably because foraging at lower and higher depths (i.e. shorter or longer travel durations) provided relatively better returns than those at intermediate depths, and/or because bottom durations were cut short or extended beyond the optimum durations due to the dynamics of active hunts (i.e. earlier or later prey captures than expected).

In other words, the birds seemed to sometimes appear to have caught a fish early and did not waste time searching and pursuing other prey, and came up sooner than predicted by the simple MVT model (Stephens *et al.* 2007), which, as should be remembered, is based on the assumption of a constant rate of gain. They also seemed to stay longer than predicted, presumably pursuing elusive prey, because once having located a rare prey it may have not been worth giving up the chase and returning to the surface at the 'optimal' time as predicted from an MVT with continuous gain. The premature termination of some WBD dives may also have been the result of trying to end such dives closer to the optimal dive cycle ratio as predicted by the more complex MVT model of Walton *et al.* (1998). The optimal bottom duration to travel duration predicted from Clarke's (2007) simplistic MVT model (see below), should be equal to the maximized bottom durations to the lowest travel duration in Fig. 12. For females, this meant that the optimal bottom duration of 12.49s, by 19.80s of travel duration would add up to a total of 32.29s, passing the optimal dive duration to travel duration peak ratio in WBD dives by 8.83s. An overshoot of >10s were detected in males for WBD dives in both DCB and DCA. In other words, dives that seem prematurely ended in a bottom duration maximizing perspective may in fact be an attempt to optimize the dive duration to surface duration ratio (i.e. in NBD dives), whilst dives with foraging should optimize bottom duration to the travel duration of the dive (i.e. in WBD dives).

Prediction of optimal foraging duration by travel duration:

Given the number of deviations from the predicted bottom duration values (see above), it is also worth examining some of the assumptions of the MVT, either in the simple Clarke (2007) or complex Walton *et al.* (1998) versions. One of the main assumptions behind the analysis here was that the energetic demands were the same in traveling and foraging, and thus the proportions of travel to bottom durations would not matter. Yet, this assumption is unlikely to be the case. According to Williams *et al.* (2012), descending is thought to be harder work, and one reason for diving deep is due to the greater hydrodynamic drag of smaller depths (Squire 1957), which a bird descending needs to overcome. Horizontal movement is assumed to be quite low-cost swimming compared to descending, and ascending should involve mostly pure lift by buoyancy (Watanuki, *et al.* 2005), and thus more or less a free ride. In the end, however, in these analyses the high cost descent and low-cost ascent are combined into a total travel duration, which may in fact be comparable to the intermediate cost of swimming during bottom duration, and so the MVT assumption in this regard is not obviously incorrect.

The correlation between predicted and observed bottom durations proved significantly positive (though <60%), but there were an extensive number of deviations from the line. This was expected for several reasons; short bottom durations and the large amount of more or less absent surface durations (seen as scatter below the curve in Fig. 9) may have affect how the predicted bottom duration was estimated. This is probably part of what reduced the correlation tests.

When it comes to the extremely short surface durations, the most plausible explanation (besides equipment error or an error in the DiveMove algorithm, Luque, 2007) could be that these are dives with semi-horizontal movement around the 1m depth. Due to the surface calibration, a dive ended when the logger is moved above the 1m threshold, and likewise a new dive is registered when moving below. Small changes in direction during ascent could perhaps lead to the registration of surfacing while the bird is still submerged. Similarly, they could be actual hunts close to the surface, and although less likely, surfacing where the bird is too eager to take a break besides maybe taking one breath (e.g. dropping prey when surfacing). Due to the exponential increase of the curve in Fig. 9 and the fact that dive duration is included in both axes, along with surprisingly short surface durations for many of the dives, optimal dive durations that were shorter than the subtracted observed travel duration predicted bottom durations with impossible lengths. In fact, all dive durations below 33s returned negative travel durations that resulted in bottom durations longer than the total dive duration, which suggests some sort of methodological issue. The issue arose as an artefact of optimal dive duration being based on its predicted exponential relationship with dive cycle (see above).

An additional issue in the correlation was the large proportion of short bottom durations around a few seconds or less; barely enough for a shag to change direction before returning to the surface, and probably not enough time to chase and catch prey. Thus, many of these WBD dives may in reality have been NBD dives, with a large turning radius between descent and ascent recorded as a bottom duration. This issue could probably be avoided by using TDR loggers with a salt water switch to registrate dry (i.e. in air) and wet (i.e. submerged) periods, but then the logger may need to be fitted on the shags in another way, due to its rear end usually being lowered in the water as it floats.

The effect of body mass in a Marginal Value foraging system:

Body mass did not have a significant effect on the second order polynomial curve of bottom duration explained by travel duration, neither alone nor as interaction. This is unsettling, considering that, as predicted by MVT, we found that large individuals (i.e. males) chose to dive deeper and for longer than the smaller individuals (i.e. females), thus, they are predicted to endure longer foraging durations (i.e. bottom durations). Further, the MVT predicts that as larger individuals have longer travel durations they should choose fewer foraging trips (i.e. fewer longer dives in a bout), which we determined for males compared to females. However, the effect of body mass in the MVT system was only tested in a highly complicated analysis, with a poorly fitted second order polynomial curved model. Thus, the effect of body mass should be investigated further; Especially because body mass should influence the shape of the diminishing returns implied in the MVT, because of a mass-dependent effect on the increased costs for each successive time period spent foraging, in this case due to decreasing uptake rates of O_2 per time on the surface (see Introduction). Further, body mass should influence certain physiological or environmentally based rules inherent to the MVT predictions, such as O_2 uptake and storage capacity, buoyancy, hydrodynamic drag, and perhaps even size and density of prey at the different depths achievable by different sized shag parents.

One way to test the effect of body mass in a known procedure would be to include groupings of body masses as a factor in the piecewise linear regression model, or even fit a curve for each individual, with indications of weight class or body mass to compare (see Future research). Body mass should further influence the shape of the diminishing returns implied in the MVT, because of a mass-dependent effect on the increased costs for each successive time period spent foraging, in this case due to decreasing uptake rates of O_2 per time on the surface (see Introduction).

The finding of no effect of body mass in bottom duration by travel duration provided the second sex-specific difference that could not be explained even partly by body mass. Notably, the first sex-specific trait found was how males spent more time on the surface than could be explained by their dive duration and body mass, and so there could be a connection. As discussed above, the increased surface duration in males could be a strategy to save energy (and perhaps recovering body temperature) whilst waiting for prey to return (especially after a successful hunt suggesting prey may return). According to the MVT an individual should maximize the rate of gain per time (i.e. time spent away from the nest), and so any additional time spent on the surface would have to be compensated for when foraging, thus returning a larger bottom duration per travel duration, not directly explained by body mass.

The optimal dive to surface ratio:

Our approach in determining the O_2-store utilization, using piecewise linear regression on the effect of travel duration of bottom duration showed that there was a definite peak, as predicted. The finding neatly backs up the assumption of switch metabolism by Houston and Carbone (1995), along with the previous analysis in this thesis showing that post-dive duration does not increase with dive type even though dive duration does. We did not find any second elevation in longer dive durations, but rather a sub-optimal distribution of dive duration to increase traveling duration, supporting the idea that the ADL was not crossed as a rule, and that mixed metabolism (and thus profound dive response) was unlikely to occur in a profound manner.

As determined above, the diving shags respiratory O2 -stores are depleted first, and so Walton *et al.*'s (1998) re-uptake rate with a kink (see Introduction) provides a more realistic version of the MVT as compared to the continuous uptake assumed when fitting an exponential curve to the dive cycle (Stephens *et al.* 2007).

We presented two ways of testing the peak ratio, one graphical and interval based model, similar to that by Walton *et al.* (1998), and one more statistical and based on piecewise (i.e. broken-stick) linear regression. The piecewise regression shows the non-continuous change in slopes neatly, but is guilty of pseudo-replication in the sense that all intervals within and among individuals are weighed equally when they contain very different amount of observations (i.e. random effects are not possible in piecewise regression). In fact, the number of observations were as low as 1-2 observations in some interval groupings, and above 2000 observations in others.

Unfortunately, this pseudo-replication may have affected the positioning of the dive to surface peak ratio to lower dive durations, because the piecewise linear regression could not take the groupings of data into consideration. Thus, as smaller individuals had a higher number of dives per bout, and longer bouts with higher frequency of NBD dives, smaller individuals would have been overly represented in the shorter dive duration intervals. Further, longer dive durations may be dominated by larger individuals with higher ratios.

The existence of a peak ratio (maximum dive duration gained for minimum surface duration) was evident, though at quite low dive durations. Walton *et al.* (1998) estimated the dive to surface peak ratios to appear within 30-50s dive durations, but our estimation is lower, possibly partly due to the pseudo-replication of the piecewise regression favoring individuals with short dive duration (see above). Further, the larger intervals on the graphs used by Walton *et al.* (1998), due to their smaller data set compared to ours, makes their estimates much rougher and harder to compare to. Notably, Walton *et al.*'s maximum dive durations were longer than ours (170-190s, compared to our sample with maximum dive length of 130s for females and 158s for males, see Fig. 14a-b). There could be multiple biological reasons for the difference in peak ratio between the colonies, depending on body mass, prey type, prey abundancy and depth, foraging locations, brood demand, sex of birds, etc.

The observed variation in dive to surface ratio:

There was an increase in ratio before the peak ratio which was steeper than the decrease to the right of the peak ratio. The decelerating slope after the peak ratio fitted neatly to the expectations of the blood and tissue O_2 stores that needed to be replenished after longer dives, implying that the uptake rate of O_2 to body stores after the peak ratio was decreased. The results all together support the kinked O_2 uptake rate suggested by Walton *et al.* (1998) that separates between the fast uptake rate of O_2 into the respiratory system, and the much slower replenishment of O_2 into the blood. This contrasts with the smooth diminishing return curve predicted by Clarke (2007) - see Introduction. Further, the increase in dive to surface ratio was steeper in WBD dives than in NBD dives for both sexes. The difference in steepness, leading to a peak ratio earlier in WBD dives than NBD dives, can perhaps be explained by the higher metabolic rate in hunting dives due to increased swimming speed (Fish, 2000), leading to a more rapid depletion of respiratory O2 stores.

In Fig. 13, a wide plateau of peaking ratio in dive to surface ratio was found, which could reflect the variation of peak ratios within as well as between individuals (effect depending on number of observations per ID). The plateau may, thus, be a result of multiple peak ratios for different individuals and under varying conditions, that makes the peak of the ratio seem less abrupt than it was thought to be. One way to confirm or reject the hypothesis of such a plateau would be by calculating individual break points and then comparing them to the individual’s body mass, or even calculating break points for each dive order and then see if they vary with fatigue or decreasing body temperature (see Future Analysis below).

It follows that if NBD dives really are sampling dives then these should in theory end close to the peak in the dive cycle ratios, as the peak ratio would provide the maximum dive duration without increasing surface duration beyond the time needed for replenishing respiratory O_2 stores. We found that diving durations in NBD dives for both sexes indeed had a tendency to cluster around the peak ratio, and that the median for dive durations were closer to the peak ratio in NBD dives than in WBD dives, indicating a behaviour closer to the presumed optimum in NBD- dives. Even so, NBD dive durations often exceeded the dive duration for peak ratio.

The excessively long NBD dives with what appear to be sub-optimal ratios could possibly be explained as a hunting tactic of flushed prey up towards the surface, failed vertical pursuits of prey, or one last excessive search before moving to a different patch. However, if these were excessively long searches then the dives would have required longer post-dive durations (i.e. ending a bout), meaning that the shag could only try again after more than 360s had passed, and so excessive searching is less likely in being obviously sub-optimal. Alternatively, these birds could just have been performing longer NBD dives when they perceived the chances of possible prey being close were high – i.e. when it was especially uncertain whether the NBD dive would turn into a WBD dive or not, again assuming that the birds doesn’t plan the dive type beforehand (see above).

Additionally, the peak ratio was greater in WBD dives, which may be mainly due to an increased preparation during the pre-dive duration (see Discussion above), where the shags could dive for the same dive duration as in NBD dives, but with a lower connected surface duration. Note that there was no direct effect of sexes, but an interaction between sex and dive type, perhaps reflecting the finding that males may prepare for maximum dive duration in every pre-dive duration while females may distinguish between preparing for an NBD and a WBD dive.

The peak ratios in Figs 13 and 14 reveal the optimal dive duration to minimize surface duration, gaining most foraging duration for the cost of restoring O_2 (Walton *et al.* 1998). The MVT predicts the dive to surface peak ratio to appear at an earlier dive duration in small individuals compared to large ones, because a small O_2-stores would be depleted faster than a big one, if they did the same amount of work (i.e. diving to the same depth, under similar conditions, hunting similar prey). A larger individual had to move more mass, but a smaller individual may have a larger intrinsic metabolic rate once allometry is considered (Schreer & Kovacs 1996). However, there was no effect of sex on the dive to surface ratio, which implies that there may not be any effect of body mass, either (this could not immideately be tested, as the piecewise linear regression was unable to handle continuous fixed effect of body mass). A plausible explanation for a lack of a body mass effect could be that the increase in dive duration would be equally reflected as increase in surface duration, as the relationship between usage and replenishment was directly due to the size of the stores with similar proportions between pulmonary storage, uptake surface area and blood/tissue stores, where duration is determined by gas-transport rate. There was, however, a sex difference in the dive cycles, but if that difference was due to an effect of difference in body mass, the dive to surface peak ratio could still be expected to be similar for the two sexes within the same range of dive numbers, as the effect of body mass seemed tied to the bout length (see Discussion above).

Finally, it should be noted, again, that the method for piecewise linear regression analysis may not have been perfect. The break-points were suggested by log-likelihood estimated break points, and only these break-points were accepted. A better way to conduct such analysis for the whole data set would be by hand, using mixed models and multiple iterations of pairs of models on either side of the break point, but this would have taken too much time for it to be included in this thesis.

Future research:

Further investigation of temperature and metabolic rate:

During a diving bout two main areas of heat loss is interesting: the skin temperature for heat loss due to surrounding water temperature and heat transfer, and core/ stomach temperature to measure the effect of cold ingested prey (see above). Much of the MVT effects discussed above concern oxygen used in diving (see Introduction), but there are also predictions for body temperature declines during dives in cold water and recovery of normal body temperatures with more time on the surface (Quintana 2007), all of which suggests an alternative MVT analyses based upon thermoregulatory costs of foraging in this system. From the MVT perspective regaining resting levels of body temperature after a dive may follow the same pattern of diminishing returns as for O_2 storage with an increasing effect of dive duration on surface duration and/or dive cycle round-trip durations. A small decrease in body temperature may lead to a short surface duration, but as body temperature decreases further the corresponding surface duration may increase exponentially. The same may be true even if the body core does not get colder, due to an increased metabolic demand of thermoregulation which may shorten dive duration and increase the corresponding surface duration, thus respirometry or blood-O_2 samples may be useful for determining differences in metabolic rate.

Interestingly, the curve should perhaps be much steeper for WBD dives where prey are caught, as the ingestion of cold prey has been proven to reduce core temperature by multiple degrees centigrade (Kato *et al.* 1996). Further, Kato *et al.* (1996) described how shortly after ingesting cold prey, the body temperature would rapidly increase to heat the ingested food rapidly. Body temperature could be tested further in the theorem by taking additional measures of blood oxygen (to look for change in metabolic demand) and body or skin temperature to examine the issue of getting too cold after longer or many successive dives, or even the metabolic cost of increased thermoregulatory demand to avoid excessive cooling. This could be established by seeing if the dive to surface peak ratio is pushed to the right (i.e. meaning that there is a lowered metabolic demand due to cooling of body) or the peak ratio could be shifted to the left, indicating an increased metabolic cost of thermoregulation leading to faster emptying of O2-stores.

Finally, thermal issues are interesting from the perspective of metabolic costs due to thermoregulation, but also due to the energy that could be saved when metabolic processes slow down with decreased body temperature. The relationship of changing body temperature to dive duration, depth and bout length should be investigated, as well as how it affects the order of dives, and perhaps the proportion of NBD to WBD dives. Further, a thermal logger fitted in the stomach could reveal the true nature of NBD's and WBD's, where a cold prey should be detected as rapid decrease in temperature.

Further analysis of MVT on foraging:

With the newly gained insight in the nature of diving behavior in this system, the MVT needs to be more thoroughly tested in light of analyses on consecutive dive bouts, locations and the entire foraging trips. In addition, we need to quantify the cumulative time spent actively foraging per trip for comparison as an estimate of the total biomass of prey delivered to the nest, which could be confirmed using the overall growth rate of chicks (i.e. data that was no analyzed as part of this project). We expect that it is the time spent actively foraging at more distant and secondary locations in each trip that is important, because this is more likely to represent foraging time for chick-feeding (Ydenberg & Davies 2010). The smaller this proportion of active foraging time is at a given location that is used across different days and years, the lower the prey availability is expected to be and the predicted lower the rates of chick growth at all nests at that time. As part of this will be the preferential use of the best foraging sites at any one point in time (i.e. we do not expect data from unprofitable locations), and so systematic shifts in the locations visited are predicted for all birds monitored within and between years. Hence, the proportion of time spent actively foraging at all of these best locations should reflect the best prey delivery rates possible by parents at that time, and therefore should explain temporal variation in chick growth at the shag colony.

The large effect location had on bout lengths, may indicate self-feeding patches for parent shags, where the adult catches fewer, larger prey for themselves. By testing bout number in location against location number used per trip, and the proportion of NBD to WBD dives, a self-feeding patch should reveal itself as an early patch with few dives and bouts (or even just short in-location time), and a large proportion of WBD to NBD dives. Self-feeding should be executed earlier in longer trips to make sure the larger prey are digested as much as possible before the return to feed the chicks.

The stochasticity in distribution of a shags prey may also affect how the birds choose bout lengths at a given location. The bout lengths were largely explained by the location, and length of dive duration and maximum depth were affected by the order of dives within a bout. Thus, the location seems to directly and indirectly have a high impact on the diving strategy. It would be interesting to distinguish the variation between the locations in detail, perhaps to look for signs of self-feeding patches in the beginning of a travel and chick provisioning locations afterwards.

By sampling blood O_2 levels from shags before and after dives of different lengths, and of birds with different body masses, the true optimal dive to surface relationship could be found. Blood O_2 levels compared to resting levels could indicate if the ratio peak (subsection 2C) indeed appears at the start of blood O_2 depletion (i.e. during the early dive with respiratory O2-usage, the blood O2-levels should be equal to resting levels up to the point of peak ratio), determining whether the ratio analysis actually reveals the optimal ratio. By calculating individual peaks in the dive duration to surface duration ratios (see above and Walton *et al.*, 1998) it should be possible to compare them to variation in individual body mass, which is predicted to have a positive effect if the physiological mechanisms here are operating as expected. Similarly, calculating these peaks for each dive order within a bout could reveal whether there were any effects of fatigue, or even thermal issues of heat loss (see above) – i.e. the peak ratio moving to the left if the heat loss leads to an increased cost of thermoregulation, or moving to the right if heat loss leads to reduced metabolic costs.

Further, the question of whether dives are planned prior to- or during a dive could be resolved out by monitoring heart rates and connecting them to TDR data of dive type and dive duration, to look for effects of preparation for a dive, the dive type and dive duration. In female shags, a lower mean heart rate would be expected in NBD- pre dive durations, than in WBD predive durations, revealing a difference in dive preparations between dive types. The preparations in male shags are predicted to be similar between dive types due to finding that the effect of pre-dive duration on dive duration is equal. Further, heart rates could give more information on the effect of order of dives on fatigue (i.e. heart works harder and takes longer to return to normal beating frequencies with increasing dive duration).

Finally, the effect of body mass could be tested in the change in heart rate, to investigate allometric differences in metabolism in dives with similar duration. Heart rate data could additionally be tested for difference between individuals in bottom durations at similar depths, to reveal if larger individuals seek deeper depths to avoid cost of transport in shallow water, and to see if cost of transport actually diminishes at a certain depth for medium-large individuals (see discussion above).

Conclusion:

In the end, our three main hypotheses were supported with new findings, though some of our predictions (i.e. short bout lengths for small individuals and increasing surface durations towards the end of bouts) was rejected, in favour of even more interesting and nuanced solutions to foraging shags than first thought. Several different strategies for preparation before a dive, decision on dive type and size specific niches within a sample population was suggested, based on these findings. Most interesting were perhaps to find evidence for a sex specific hunting strategy that here could not be tied directly to the effect of body mass. Our findings suggest that the sexes chose to follow prey in opposite directions in the water column as the number of dive (in a sequence of dives) increased, where females chased prey towards shallower depths, and males chased prey into the deep. All further main results were based on the differences between sexes, intention of dive, and the accumulating effects of order within and between sequential dives.

We found a strong effect of dive duration on the following dive cycle, concluding that uptake rate of O_2 followed a diminishing returns function in the shags. This finding indicated that the shags adjusted their surface duration to the connected dive duration, and that there would be a difference in O_2-uptake rate to the respiratory system and the blood/tissue stores.

Further, we found evidence strongly suggesting that in shorter dives the shag attempts to optimize the dive duration to surface duration ratio (i.e. in NBD dives), whilst in longer dives with foraging duration the shags attempted to optimize bottom duration to the travel duration (i.e. in WBD dives).

Following Houston and Carbone’s (1995) description, we determined that the shags respiratory O_2-stores were depleted before the onset of blood and tissue O_2-stores (aka. switch metabolism) for diving shags by investigating the peak durations in bottom duration based on traveling length. The conclusion is that there are a large variety of trade-offs determining the diving strategies in the avian forager tested. The shags were highly influenced by their body mass and facilitated by their high ability to adjust to a stochastic environment, but also findings supporting suggested sex specific strategies (with more or less effect by body mass).

We determined the dive to surface peak ratios in the two sexes for each of the two dive types describes, by using the Walton *et al.’s* dive to surface ratio-method and conclude that divers behaved closer to the predicted optimum dive durations during the presumed ‘sampling’ dives and behaved closer to the optimal foraging duration per travel duration in presumed ‘hunt’ dives. We further suggest that higher metabolic demand in ‘hunting’ dives led to the dive to surface peak ratio’s appearance in earlier dive durations, and that the higher median dive duration was the sign of a trade-off between the costs of less efficient dive cycles with extended surface durations versus the benefits of staying down sufficiently long to catch elusive fish prey.

We finally conclude that Walton *et al.*’s refinement of the MVT, with respect to the study organisms physiology, is a more accurate way of determining the time efficiency in a divers foraging. However, there are still uncovered aspects that should be attended in the future. Important effects of individual body mass on MVT predictions were not found and clear interaction effects with dive order suggest that maintaining body temperature might also be an issue in this system. Further statistical analyses are recommended that could be used to investigate these effects in light of optimality predictions and knowledge of avian physiology.

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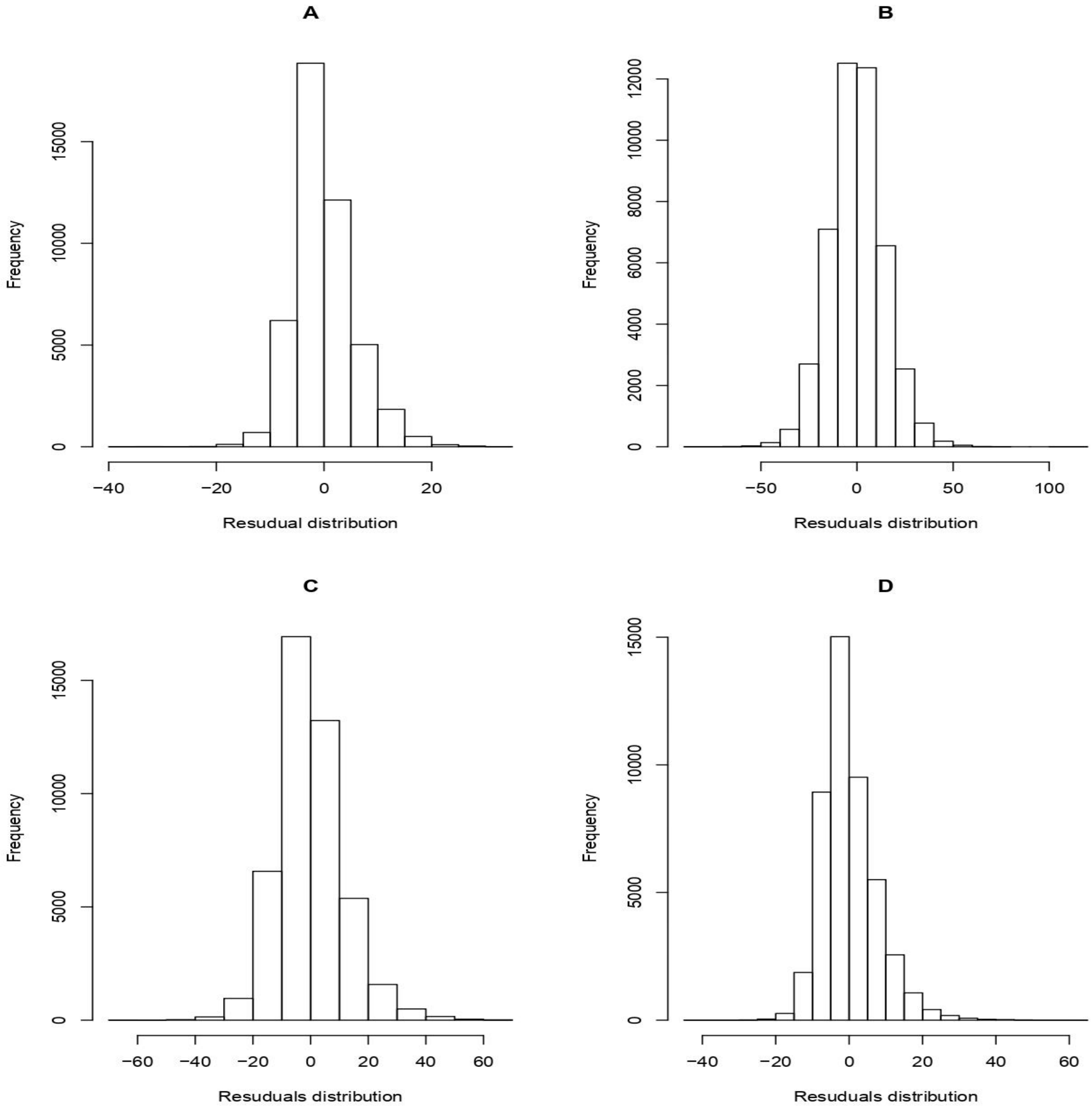
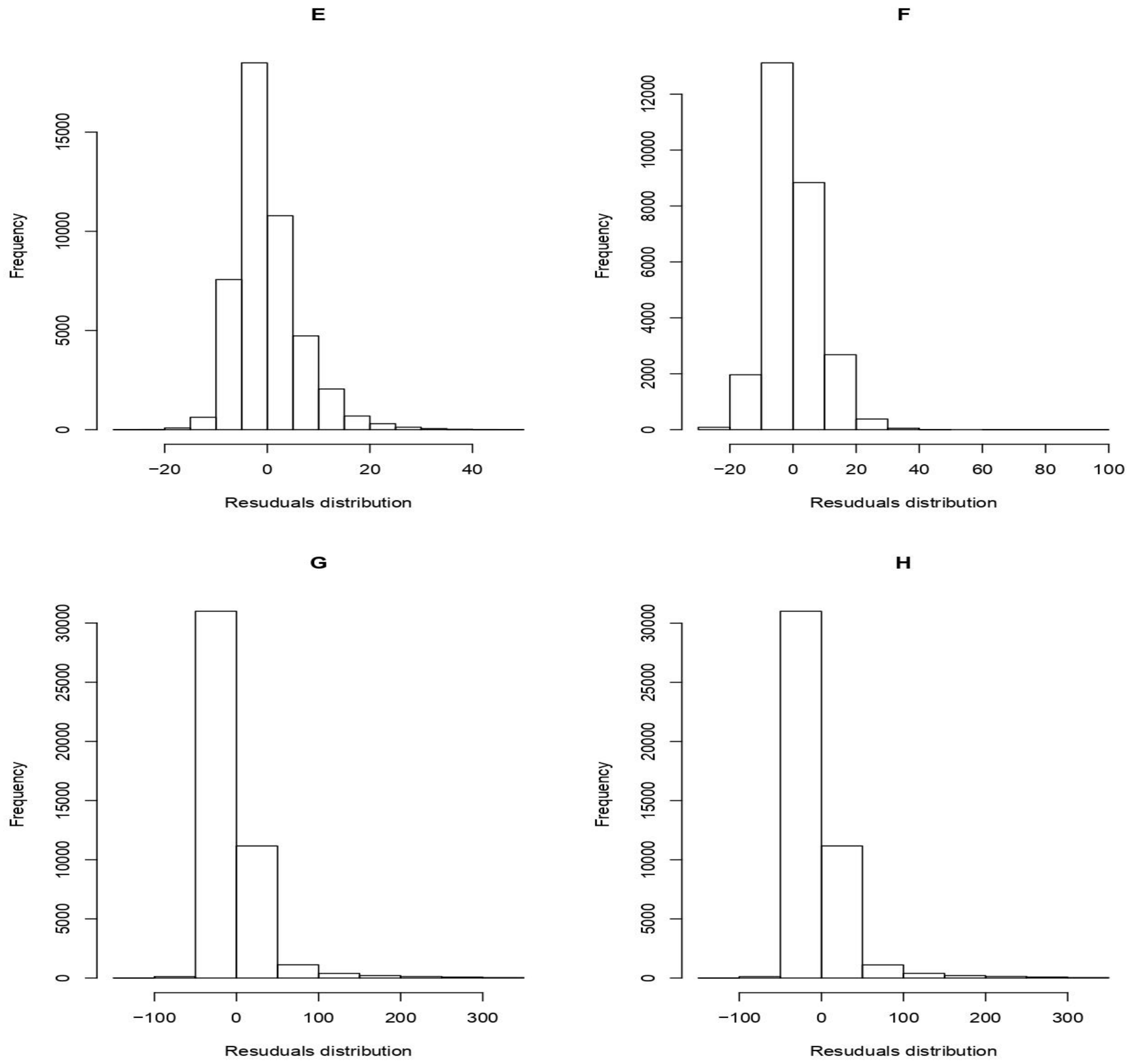
Supplementary information:

APPENDIX S1: RESIDUAL DISTRIBUTION FOR MODELS TABLE 1

Fig. S1: Residual distribution for linear mixed effect models used in table 1, with analyses based on the assumption of normal distribution. The effect of dive type and sex on main parameters: A) Maximum depth, B) Dive duration, C) Descending duration, D) Ascending duration, E) Bottom duration, F) Pre-dive duration, G) Post dive duration.




E
Frequency
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Resuduals distribution
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Frequency
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0
20
40
60
80
100
Resuduals distribution
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Frequency
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30000
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Resuduals distribution

APPENDIX S2: LOCATIONS

Table S2: Overview of locations, given as squared areas within latitudes and longitudes given. See Table S1 for description. Sub-locations were used in all analyses. Lat1= start point in latitude, Lat2= end point in latitude, Long1= start point of longitude, Long2= stop point in longitude, locations are square shaped.

Loc	Subloc	Name	Lat1	Lat2	Long1	Long2
A	0	Sklinnafleisen	65,1	65,15	10,08	11,05
A	1	Sklinnafleisen	65,1	65,15	10,08	10,9
A	2	Sklinnafleisen	65,1	65,15	10,9	10,95
A	3	Sklinnafleisen	65,1	65,15	10,95	11
A	4	Sklinnafleisen	65,1	65,15	11	11,05
B	0	Kalvøy/Rødøy	64,95	65,1	10,9	11,2
B	1	Kalvøy/Rødøy	65.05	65,1	10,9	11,2
B	2	Kalvøy/Rødøy	64,95	65.05	10,9	11
B	3	Kalvøy/Rødøy	64,95	65.05	11	11,15
B	4	Kalvøy/Rødøy	64,95	65.05	11,15	11,2
C	0		65,15	65,25	10,9	11,05
C	1		65,19	65,25	10,9	11,05
C	2		65,15	65,19	10,9	11,05
D	0		65,16	65,25	11,05	11,3

D	1		65,16	65,25	11,05	11,12
D	2		65,16	65,25	11,12	11,3
E	0	Innersklinnabanken	65,1	65,16	11,05	1140
E	1	Innersklinnabanken	65,1	65,16	11,05	11,25
E	2	Innersklinnabanken	65,1	65,16	11,25	11,4
F	0	Lekasteinan	65	65,1	11,25	11,5
F	1	Lekasteinan	65	65,1	11,25	11,36
F	2	Lekasteinan	65	65,1	11,36	11,43
F	3	Lekasteinan	65	65,1	11,43	11,5
G	0	Horsvær/Horta	65,16	65,3	11,3	11,6
G	1	Horsvær/Horta	65,24	65,3	11,3	11,5
G	2	Horsvær/Horta	65,24	65,3	11,5	11,6
G	3	Horsvær/Horta	65,16	65,24	11,3	11,6
H	0	Bremstein	65,3	65,4	11	11,1
H	1	Bremstein	65,3	65,4	11	11,05
H	2	Bremstein	65,3	65,4	11,05	11,1
I	0	Langfallet	65	65,05	10,7	11,8

APPENDIX S3: LINEAR AND POLYNOMIAL EFFECT OF BODY MASS ON MAIN PARAMETERS

Table S3: The effect of body mass on dive parameters maximum depth and different dive durations and surface durations separated by sex for (A) no bottom duration (NBD) and with bottom duration (WBD) dive types. Note that the non-linear term body mass squared is only included when significant. Mixed effect models included identity, location, year and dive date as random effects, which are given as proportions of total variation explained. Fixed effects are given as effect sizes (for non-standardized values) with 95% CIs. Bold numbers for significant values, except in intercepts.

a) NBD, FEMALES:

	Max depth	Dive duration	Descending duration	Ascending duration	Pre-dive duration	Post-dive duration
Intercept	-127.88 (-236.48, -22.26)	-497.56 (-786.17, -199. 21)	-223.79 (-376.73, -75.82)	-196.38 (-336.53, -58.65)	18.41 (-15.15, 47.13)	23.68 (-2.76, 51.09)
Mass	**0.16** **(0.03, 0.30)**	**0.61** **(0.25, 0.96)**	**0.28** **(0.09, 0.46)**	**0.24** **(0.07, 0.41)**	1.1e-3 (-0.02, 0.02)	-1.9e-3 (-0.02, 0.01)
Mass^2	**-4.5e-5** **(-8.6e-5, -5.1e-6)**	**-1.7e-4** **(-2.8e-4, -6.8e-5)**	**-8.1e-5,** **-1.4e-4, -2.6e-5)**	**-7.0e-5** **(-1.2e-4, -1.8e-5)**	**-**	**-**
ID	0.13	0.11	0.07	0.09	0.03	0.02
Location	0.14	0.24	0.15	0.13	0.01	0.00
Year	0.00	0.00	0.00	0.00	0.001	0.002
Dive date	0.09	0.07	0.05	0.06	0.01	0.01
Residual	0.63	0.56	0.71	0.72	0.94	0.96

NBD, Males

Intercept	-0.63 (-25.36, 22.46)	10.25 (-29.59, 49.66)	5.80 (-16.77, 29.35)	6.98 (-9.81, 23.03)	33.55 (-50.58, 118.15)	19.91 (-57.92, 97, 61)

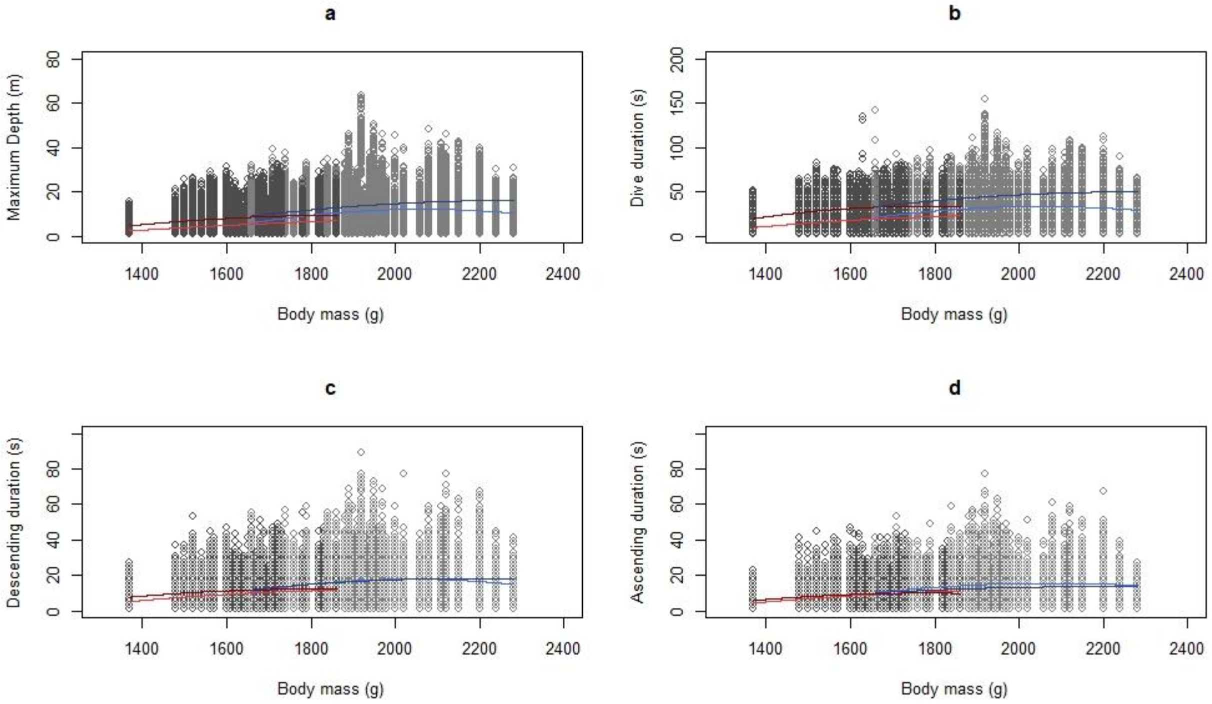
Mass	0.008 (-0.004, 0.02)	0.01 (-0.006, 0.03)	0.007 (-0.005, 0.20)	0.005 (-0.003, 0.01)	0.006 (-0.04, 0.05)	0.01 (-0.03, 0.05)
ID	0.21	0.11	0.15	0.10	0.17	0.14
Location	0.19	0.25	0.15	0.11	0.08	0.09
Year	0.07	0.00	0.05	0.05	0.02	0.03
Dive date	0.17	0.07	0.11	0.11	0.02	0.01
Residual	0.35	0.57	0.53	0.62	0.71	0.73

b) WBD, female:

	Max depth	Dive duration	Descending duration	Ascending duration	Bottom duration	Pre-dive duration	Post-dive duration
Intercept	-6.98 (-18.65, 5.65)	-456.88 (-858.27, -47.74)	-2.19 (-13.09, 8.44)	-120.75 (-216.24, -25.46)	-2.34 (-16.44, 12.21)	11.95 (-10.80, 33.96)	8.77 (-17.16, 35.27)
Mass	**0.009** **(0.001, 0.02)**	**0.57** **(0.07, 1.07)**	**0.009** **(0.002, 0.015)**	**0.15** **(0.04, 0.27)**	0.008 (-3.7e-4, 0.02)	0.007 (-0.007, 0.02)	0.01 (-0.006, 0.03)
Mass^2	-	**-1.7e-4** **(-3.2e-4, -1.2e-5)**	-	**-4.4e-5** **(-7.9e-5, -7.8e-6)**	-	-	-
ID	0.15	0.24	0.09	0.07	0.11	0.02	0.02
Location	0.16	0.10	0.10	0.18	0.11	0.05	0.07
Year	0.00	0.04	0.00	0.00	0.00	0.00	0.00
Dive date	0.06	0.18	0.03	0.02	0.04	0.01	0.01
Residual	0.62	0.44	0.79	0.72	0.75	0.92	0.90

WBD, males:

Intercept	-1.92 (-26.13, 20.56)	2.97 (-37. 81, 44.43)	2.52 (-18.06, 22.96)	5.84 (-6.65, 17.90)	-0.58 (-13.92, 12.72)	27.69 (-47.50, 101.30)	33.53 (-46.26, 113.86)
Mass	0.01 (-0.002, 0.02)	**0.02 (0.002, 0.04)**	0.009 (-0.02, 0.02)	0.005 (-0.002, 0.01)	**0.008 (5.2e-4, 0.01)**	0.01 (-0.03, 0.05)	0.007 (-0.03, 0.05)
ID	0.29	0.24	0.23	0.23	0.14	0.09	0.16
Location	0.15	0.10	0.10	0.10	0.18	0.02	0.17
Year	0.03	0.04	0.04	0.07	0.02	0.00	0.03
Dive date	0.18	0.18	0.09	0.04	0.07	0.05	0.06
Residual	0.35	0.44	0.54	0.62	0.59	0.84	0.58



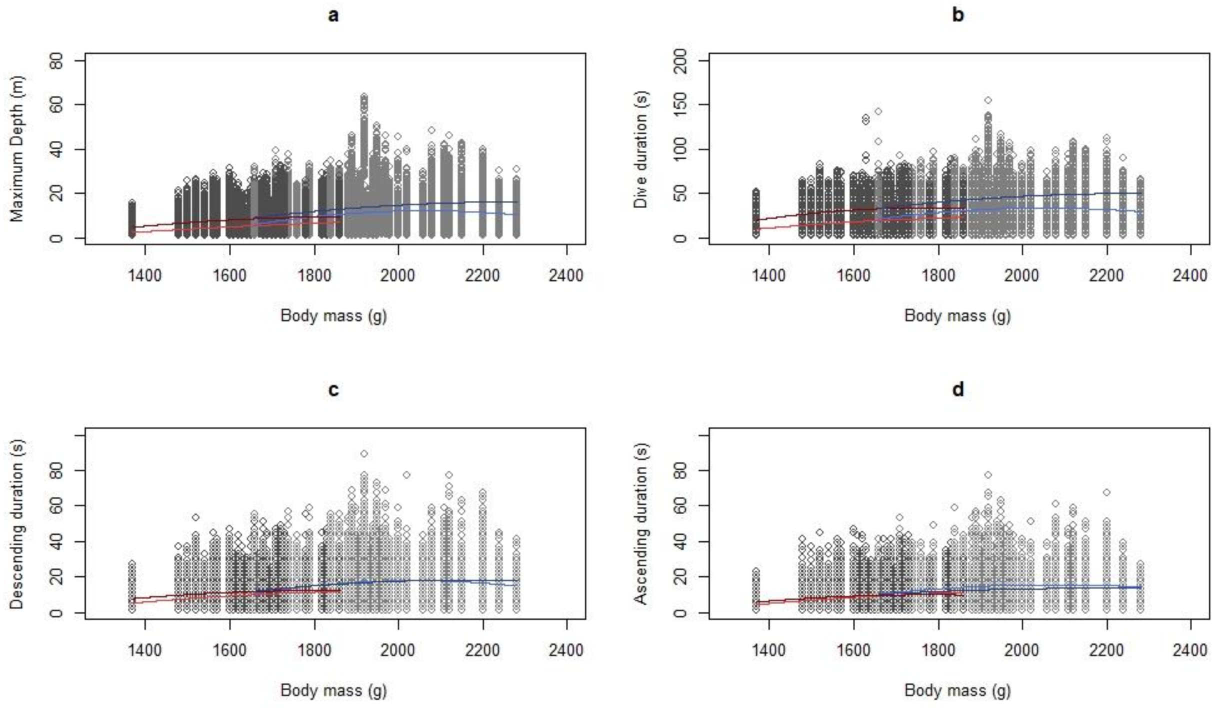


Fig. S3: Body mass effects on the different dive parameters, separated by sex (no bottom duration NBD [light colours]; With bottom duration WBD [dark colours]) and sex (female [red]; male [blue]) - see Table S3a) Maximum depth, b) Dive duration, c) Descending duration, d) Ascending duration, e) Bottom duration, f) Pre-dive duration and g) Post dive duration.

Effect of body mass (Table S3):

The continuous pattern was that body mass made a large difference for smaller individuals (i.e. females) but levelled off at a point (Fig. S3a-g), suggesting a counter-gradient effect that works against the positive effect of body mass. Considering that the estimated maximum depth of male dives increased by 3.6m from samples to hunts, it is interesting to note the increase in velocity or assumed acceleration in speed. Female birds took on average 9.85 s ascending, with a span from 7.10s (1370g) to 12.72s (1860g) as a response to body mass variation (Fig. S3d). After a hunt the average ascending to surface lasted for 10.07s, with a span from 8.01s to 12.20s (effect of body mass), much similar to the sample dives. Males spent on average 16.58s on this part of sample dives, and slightly less (15.44s) when returning from a hunt.

Body mass had large positive effect on maximum depth for no bottom duration, NBD, dives, which was also decelerating non-linear for females (Table S3a; Fig. S3a). The average NBD dive depth for males was 10.47m, and 4.84m for females, perhaps reflecting sex differences in body mass. In female NBD dives, maximum depth increased by 0.0008m per gram, which seems like a small effect size but it translates to an overall effect of mass changing dive depths from 3.87m to 7.89m, a range of 4.02m for male shags. For male NBD dives, the effect of body mass was non-significant, suggesting that at higher body mass values any increase in body mass did not have an effect on dive depth when merely sampling and not actively chasing prey. The effects of body mass on dive depth were less clear for with bottom duration, WBD, dives (Table S3b; Fig. S3a). Female WBD dives were deeper than NBD dives, ranging from 5.35m to 9.76m increasing linearly as body mass increased. WBD dive depth was also deeper than NBD dives for males by 13.42m, but again there was no significant effect of body mass on WBD dive dept. WBD dives that included horizontal prey hunts therefore required deeper dives and perhaps more random variation in depth due to the pursuit of prey not associated simply with body mass.

Dive durations also increased (but with a decelerating curve for the lighter females) with body mass in both NBD and WBD dives (Table S3; Fig. S3b). Although this largely reflected the effects (above) in maximum dive depth, the effects of body mass on dive durations seemed less affected by random noise generated due prey pursuits during WBD dives. Heavier birds of both sexes were able to perform longer NBD and WBD dives, although the decelerating nature of this effect meant that it was less evident in heavier males and the longer WBD dives. Female NBD dive durations ranged from 15.19s for the lightest individuals to 27.42s for the heaviest, with a mean of 21.13s. Male NBD dive durations averaged 29.45 s with no effect of body mass, again perhaps due to the non-linear decelerating nature of the effect, as seen in the lighter females. Dive durations were estimated to increase for WBD, to 25.54 s for the smallest individuals and 40.15 s for the largest ones, a mean mass of 32.70 s (increase of 11.57s). Male NBD dive duration lasted on average for 8.32 s, and increased to 36.17s for the smallest individuals (1660g), 48.57s for the largest one (2280g) and 41.37s (increase of 11.92s) for mean mass of male birds in hunting dives. The largest female bird is thus indeed estimated to perform at the same level as male birds in the same weight class, emphasising that the effect of sex cannot be distinguished from the effect of body mass.

Bottom duration during WBD dives was not affected by body mass in females, and was on average 10.54s (fig. S3e). For male birds there was a positive relationship between body mass and bottom duration, ranging from 12.70s to 17.66s, and so again although the effect size in Table S3b looks small larger body mass could allow males at least an additional 7 s for pursuing prey. It is not clear why this effect only appears in the heavier male birds, but there was a difference of 4 s between the bottom durations of the larger females and males of same size, which represents 50% of total bottom duration for these birds. This appears to be one of the few mass-independent effects of sex on diving behaviour in these data.

Surprisingly, there were no effects of body mass on pre- or post-dive surface durations (Table S3), presumably because any effects would have had to have been indirect via the dive duration and depths effects (above) and therefore subject to excessive noise and variation. Female surface durations for NBD dives were 18.41s and 23.68 s for pre- and post-dive durations respectively, and these decreased to 23.68 s and 8.8 s for WBD dives. Male surface durations for NBD dives were 33.6 s and 19.91 s for pre- and post-dive durations respectively, and this increased to 33.5s in post dive duration, but decreased to 27.7s for pre-dive duration in WBD dives. Note however that the confidence interval spans over +-150s, making estimates much shorter than expected.

Body mass had a decelerating effect on both the ascending and descending durations in NBD as well as WBD dives for females (Table S3; Fig.S3c & d). For WBD dives, however, the effect of body mass was much stronger on ascending durations than descending durations. Female birds spent on average 10.76s descending in sample dives, with a span from 8.17s to 13.46s (lowest to highest body mass, respectively), and the time increased to 11.50s, when changing to hunting dives, with a span from 9.50s to 13.59s (Fig. S3c). Descending duration of sample dives for male birds were on average 19.24s, and in hunt dives descending duration only increased by 0.64s, with no significant change with respect to variation in body mass in either dive type. Considering that the estimated maximum depth of male dives increased by 3.6m from samples to hunts, it is interesting to note the increase in velocity or assumed acceleration in speed. Female birds took on average 9.85 s ascending, with a span from 7.10s (1370g) to

12.72s (1860g) as a response to body mass variation (Fig. S3c). After a hunt the average ascending to surface lasted for 10.07s, with a span from 8.01s to 12.20s (effect of body mass), much similar to the sample dives. Males spent on average 16.58s on this part of sample dives, and slightly less (15.44s) when returning from a hunt. The shorter return time may suggest that the birds have moved somewhat closer to the surface during the hunt, or may be more exhausted on O2-stock and therefore putting in an extra effort hurrying to the surface.

APPENDIX S4: LINEAR AND POLYNOMIAL EFFECT OF DIVE ORDER ON MAIN PARAMETERS

Table S4: The effect of dive order on dive parameters maximum depth and different dive durations and surface durations separated by sex for (a) no bottom duration (NBD) and (b) with bottom duration (WBD) dive types. Dive order was mean centered dive number. Mixed effect models included identity, location, year and dive date as random effects, which are given as proportions of total variation explained. Fixed effects are given as effect sizes (for non-standardized values) with 95% CIs. Bold numbers for significant values, except in intercepts.

a) NBD, FEMALES:

	Max depth (m)	Dive duration (s)	Descending duration (s)	Ascending duration (s)	Pre-dive duration (s)	Post-dive duration (s)
Intercept	6.04 (4.77, 7.35)	22.12 (18.01, 26.26)	11.08 (9.14, 13.19)	10.63 (8.92, 12.34)	24.88 (21.73, 27.78)	25.55 (23.49, 27.47)
Order	**-2.68e-3** **(-3.10e-3, -3.56e-3)**	**-1.42e-2** **(-1.80e-2, -8.86e-3)**	**-5.08e-3** **(-8.77e-3, -1.57e-3)**	**-9.23e-3** **(-1.46e-2, -3.77e-3)**	**-0.11** **(-0.14, -8.38e-2)**	**-0.14** **(-0.17, -0.12)**
Order^2	-1.76e-5 (-3.16e-5, 8.54e-6)	-3.09 (-6.97e-5, 5.86e-6)	**-3.80e-5** **(-6.34e-5, -6.78e-7)**	6.56e-6 (-1.56e-5, 2.73e-5)	**2.92e-4** **(1.91e-4, 3.99e-4)**	**4.14** **(3.10, 5.16)**
ID	0.19	0.18	0.13	0.16	0.02	0.01
Location	0.13	0.16	0.10	0.09	0.01	0.00
Year	0.00	0.00	0.00	0.00	0.00	0.00
Dive date	0.01	0.06	0.05	0.05	0.00	0.01
Residual	0.62	0.59	0.72	0.71	0.97	0.98

NBD, Males

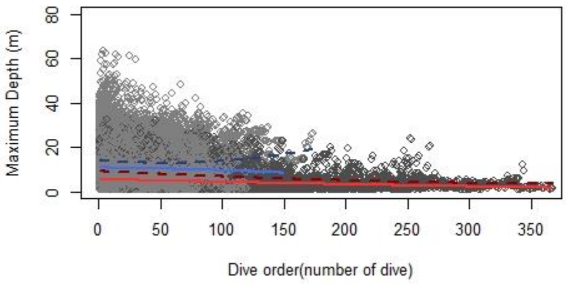
Intercept	14.14 (9.71, 18.63)	35.66 (26.94, 43.90)	18.87 (13.89, 23.71)	16.21 (12.89, 19.51)	49.16 (36.68, 61.88)	48.90 (37.98, 60.30)
Order	**2.91e-2 (1.11e-2, 4.81e-2)**	**8.22e-2 (4.00e-2, 0.12)**	**6.29e-2 (3.49e-2, 9.05e-2)**	2.05e-2 (-3.02e-3, 4.40e-2)	**-0.24 (-0.35, -0.13)**	**-0.28 (-0.38, -0.17)**
Order^2	-2.28e-4 (-4.07e-4, 1.54e-5)	**-8.90e-4 (-1.33e-3, -4.46e-4)**	**-6.51e-4 (-9.19e-4, -3.94e-4)**	**-2.52e-4 (-4.85e-4, -1.70e-5)**	**1.62e-3 (5.37e-4, 2.78e-3)**	**1.73e-3 (6.79e-4, 2.75e-3)**
ID	0.22	0.17	0.15	0.10	0.17	0.17
Location	0.18	0.13	0.14	0.11	0.07	0.07
Year	0.05	0.04	0.04	0.04	0.03	0.03
Dive date	0.22	0.21	0.16	0.10	0.01	0.00
Residual	0.34	0.45	0.51	0.65	0.73	0.76

b) WBD, female:

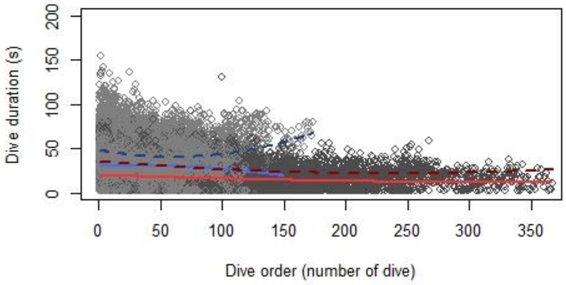
	Max depth	Dive duration	Descending duration	Ascending duration	Bottom duration	Pre-dive duration	Post-dive duration
Intercept	9.44 (7.87, 10.96)	38.47 (34.08, 42.89)	12.61 (11.50, 13.64)	10.85 (9.68, 11.97)	13.34 (11.61, 15.00)	26.66 (23.19, 30.24)	26.70 (23.09, 30.56)
Order	**-1.39e-2 (-1.78e-2, -9.99e-3)**	**-8.46e-2 (-9.39e-2, -7.50e-2)**	**-1.92e-2 (-1.86e-2, -1.42e-2)**	**-1.82e-2 (-2.19e-2, -1.48e-2)**	**-4.73e-2 (-5.31e-2, -4.14e-2)**	**-5.59 e-2 (-6.79e-2, -4.39e-2)**	**-7.42e-2 (-9.77e-2, -4.98e-2)**

Order^2	**1.63e-5 (2.61e-7, 3.33e-5)**	**1.69e-4 (1.24e-4, 1.12e-4)**	**2.44e-5 (2.80e-6, 4.42e-5)**	**3.37e-5 (1.87e-5, 5.03e-5)**	**1.10e-4 (8.68e-5, 1.36e-4)**	**2.63e-4 (1.72e-4 , 3.59e-4)**	**1.68e-4 (6.43e-5, 2.74e-4)**
ID	0.21	0.21	0.11	0.10	0.12	0.02	0.02
Location	0.15	0.20	0.05	0.12	0.08	0.04	0.04
Year	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dive date	0.03	0.02	0.01	0.01	0.02	0.00	0.00
Residual	0.62	0.57	0.84	0.77	0.78	0.94	0.94
WBD, males:							
Intercept	16.76 (13.41, 20.16)	50.54 (44.17, 56.83)	19.92 (17.08, 23.05)	14.80 (12.54, 16.89)	15.65 (14.16, 17.21)	48.74 (37.74, 60.80)	47.70 (36.10, 59.88)
Order	**-3.50e-3 (-1.42e-2, -6.95e-3)**	**-0.17 (-0.19, -0.14)**	**-2.47e-2 (-3.84e-2, -1.17e-2)**	**-1.52e-2 (-2.08e-2, -1.03e-2)**	**-0.12 (-0.14, -0.11)**	**-0.12 (-0.18, -0.06)**	**-8.96e-2 (-0.15, -2.83e-2)**
Order^2	**1.18e-4 (9.71e-7, 9.84e-5)**	**1.08e-3 (8.50e-4, 1.30e-3)**	**1.16e-4 (1.80e-6, 2.41e-4)**	**9.06e-5 (4.39e-6, 1.84e-4)**	**8.80e-4 (7.47e-4, 1.02e-3)**	3.67 e-4 (-1.66e-4, 8.92e-4)	2.27e-4 (-3.13e-4, 8.20e-4)
ID	0.30	0.25	0.17	0.14	0.10	0.17	0.20
Location	0.15	0.11	0.12	0.16	0.02	0.13	0.13
Year	0.01	0.01	0.02	0.02	0.01	0.01	0.03
Dive date	0.19	0.19	0.08	0.06	0.01	0.03	0.01
Residual	0.35	0.44	0.56	0.62	0.86	0.65	0.63

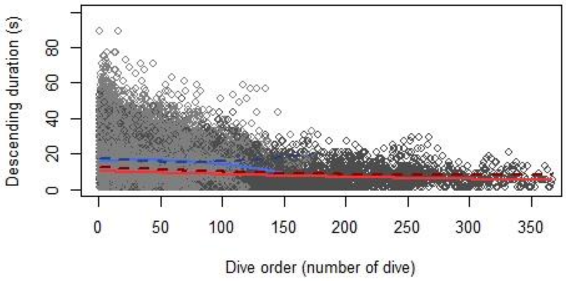
a


Maximum Depth (m)
0
20
40
60
80
0
50
100
150
200
250
300
350
Dive order(number of dive)

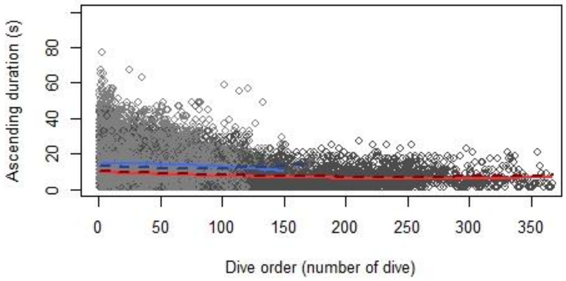
b


Dive duration (s)
0
50
100
150
200
0
50
100
150
200
250
300
350
Dive order (number of dive)

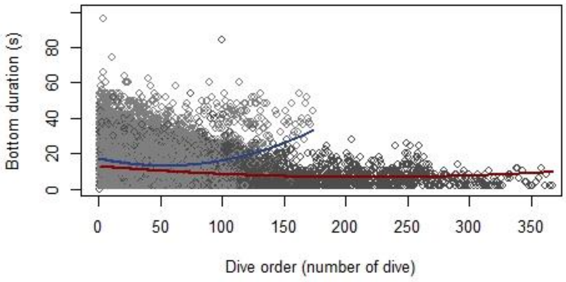
c


Descending duration (s)
0
20
40
60
80
0
50
100
150
200
250
300
350
Dive order (number of dive)

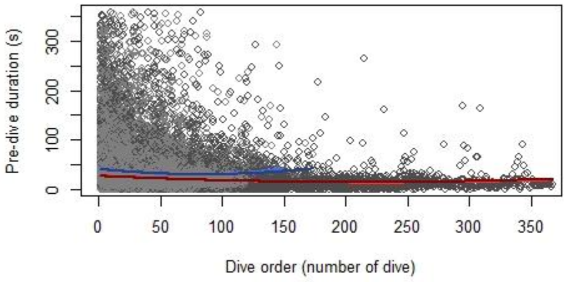
d


Ascending duration (s)
0
20
40
60
80
0
50
100
150
200
250
300
350
Dive order (number of dive)

e


Bottom duration (s)
0
20
40
60
80
0
50
100
150
200
250
300
350
Dive order (number of dive)

f


Pre-dive duration (s)
0
100
200
300
0
50
100
150
200
250
300
350
Dive order (number of dive)

g

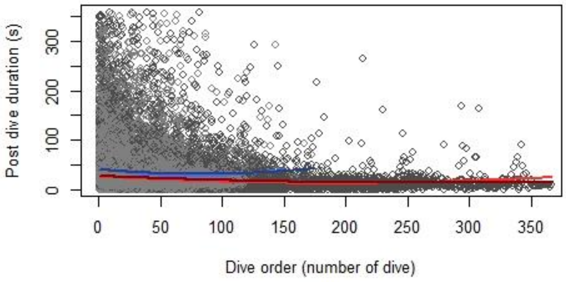

Post dive duration (s)
0
100
200
300
0
50
100
150
200
250
300
350
Dive order (number of dive)

Fig. S4: Dive order effects on the different dive parameters, separated by sex (no bottom duration NBD [light colours]; With bottom duration WBD [dark colours]) and sex (female [red]; male [blue]) - see Table S4. A) Maximum depth, B) Dive duration, C) Descending duration, D) Ascending duration, E) Bottom duration, F) Pre-dive duration and G) Post dive duration. See Table S4.

Effect of dive order (Table S4):

The mean-centred order of dives in a sequence of dives (dive order) had over all much impact on female NBD dives (table S4a; Fig S4A-F). The effect was significantly negative for all dive parameters (Fig.S4A-D), with a curvilinear relationship in descending duration along with surface durations (Fig.S4E&F). This implies that NBD dives become shallower and shorter for each sequential dive in a bout, and that surface durations are responding by becoming shorter too. There was still a decrease in depth and duration for female WBD dives (Table S4b), but with a decelerating effect over longer orders for all parameters. Fatigue could be determining factor, were it not for the additional negative effect of dive order on surface durations.

Interestingly, male NBD- dives only increase in depth and length for all parameters (table S4a; Fig S4A-F) except ascending duration and surface durations (Fig.S4E&F). This suggests that males increase their effort in sample dives towards the end of a bout, but that surface durations respond by becoming shorter, perhaps signalling impatience to switch patch if no further prey is located. In contrast, there was a strong negative effect on the same parameters in males WBT dives (Table S4b; Fig.S4E&F), with decreasing lengths of surface durations with dive order. This suggests that the differences in dive parameters between the two dive types became smaller in longer dive bouts, perhaps as more information had been sampled, dives became less random (i.e. at around bouts of 110 dives, male WBT and NBT dives would be at approximately the same depth of 16.5m).

APPENDIX S5: EFFECT SIZE OF SEX AND BODY MASS

Table S5: General sex and body mass differences with CI. Body mass effect based on 300g increase (mean difference between male and female individuals), from estimates based on body mass effect for females (See methods). Bold numbers for significant values, except in intercepts.

	Maximum depth (m)	Dive duration (s)	Descending duration (s)	Ascending duration (s)	Bottom duration (s)	Pre-dive duration (s)	Post dive duration (s)
Sex	**-4.92 (-6.95, -2.85)**	**-11.12 (-15.41, -6.82)**	**-5.06 (-7.00, -3.24)**	**-3.55 (-4.90, -2.34)**	**-3.34 (-4.74, -1.96)**	**-12.90 (-19.47, -6.44)**	**-13.20 (-20.09, -6.55)**
Body mass (per g)	**4.20 (1.71, 6.72)**	**13.47 (5.04, 21.39)**	**4.17 (1.52, 6.66)**	**3.81 (1.65, 5.85)**	**3.51 (0.50, 7.35)**	3.03 (-1.93, 7.35)	3.09 (-1.55, 7.59)

APPENDIX S6: EFFECT OF DIVE TIME ON DIVE CYCLES AND SURFACE TIMES (EXPONENTIAL MODELS)

Table S6: Finding the parameters for intercept and slope in logDCB (log pre-dive duration-based dive cycle) (a), logDCA (post-dive duration based dive cycle) (b), log pre-dive duration (c), and log post dive duration (d) of dive duration, separated by sex for no bottom duration (NBD) and with bottom duration (WBD) dive types. Mixed effect models included identity, location, year and dive date as random effects, which are given as proportions of total variation explained. Fixed effects are given as effect sizes (for non-standardized values) with 95% CIs. Bold numbers for significant values, except in intercepts.

a) Finding the exponentials for DCB (pre-dive duration-based dive cycle) by dive duration.

	Female NBD	Female WBD	Male NBD	Male WBD
Alpha	2.80 (2.72, 2.88)	2.93 (2.88, 2.99)	3.08 (3.01, 3.33)	3.28 (3.22, 3.33)
Beta	**3.43e-2 (3.34e-2, 3.51e-2)**	**3.00e-2 (2.96e-2, 3.04e-2)**	**2.81e-2 (2.73e-2, 2.34e-2)**	**2.30e-2 (2.26e-2, 2.34e-2)**

b) Finding the exponentials for DCA (Post-dive duration based dive cycle) by dive duration.

	Female NBD	Female WBD	Male NBD	Male WBD
Alpha	2.80 (2.76, 2.84)	2.92 (2.86, 2.98)	3.00 (2.95, 3.05)	3.17 (3.11, 3.23)
Beta	**3.52e-2 (3.43e-2, 3.61e-2)**	**3.10e-2 (3.06e-2, 3.14e-2)**	**2.96e-2 (2.89e-2, 3.02e-2)**	**2.52e-2 (2.48e-2, 2.56e-2)**

c) The effect of the exponential relationship between DCB (Pre-dive duration-based dive cycle) by dive duration

	Female NBD	Female WBD	Male NBD	Male WBD
Intercept	2.80 (2.72, 2.87)	2.94 (2.88, 2.99)	3.08 (3.01, 3.15)	3.28 (3.22, 3.33)
Dive duration (S)	**3.43e-2 (3.33e-2, 3.51e-2)**	**3.00e-2 (2.95e-2, 3.04e-2)**	**2.81e-2 (2.73e-2, 2.88e-2)**	**2.30e-2 (2.26e-2, 2.34e-2)**
ID	0.03	0.02	0.02	0.04
Location	0.03	0.06	0.02	0.05
Year	0.00	0.00	0.00	0.00
Dive date	0.01	0.00	0.00	0.01
Residual	0.93	0.92	0.96	0.90

d) The effect of the exponential relationship between DCA (Post-dive duration-based dive cycle) by dive duration

	Female NBD	Female WBD	Male NBD	Male WBD
Intercept	2.80 (2.76, 2.97)	2.92 (2.86, 2.97)	3.00 (2.95, 3.05)	3.17 (3.12, 3.23)
Dive duration (s)	**3.52e-2** **(3.43e-2, 3.61e-2)**	**3.10e-2** **(3.06e-2, 3.14e-2)**	**2.96e-2** **(2.88e-2, 3.03e-2)**	**2.52e-2** **(2.48e-2, 2.56e-2)**
ID	0.03	0.02	0.02	0.06
Location	0.00	0.07	0.00	0.09
Year	0.00	0.00	0.01	0.00
Dive date	0.01	0.01	0.00	0.01
Residual	0.96	0.90	0.97	0.84

APPENDIX S7: THE EFFECT OF TRAVEL DURATION ON BOTTOM DURATION

Table S7: The effect of travel duration on bottom duration, separated by sex. Mixed effect models included identity, location, year and dive date as random effects, which are given as proportions of total variation explained. Fixed effects are given as effect sizes (for non-standardized values) with 95% CIs. Bold numbers for significant values, except in intercepts.

	Female WBD	Male WBD
Intercept	1.18 (-0.47, 2.76)	9.41 (7.30, 11.76)
Travel duration (s)	**0.87 (0.83, 0.91)**	**0.36 (0.33, 0.41)**
Travelduration^2 (s^2)	**-0.015 (-0.016, -0.0014)**	**-0.006 (-0.006, -0.005)**
ID	0.09	0.14
Location	0.08	0.05
Year	0.00	0.01
Dive date	0.01	0.02
Residual	0.82	0.79

APPENDIX S8: PIECEWISE LINEAR REGRESSION FOR EFFECT OF TRAVEL DURATION ON BOTTOM DURATION

Table S8: The effect of travel duration on bottom duration, indicating one peak. Piecewise linear regression models, separated by sex. Effects are given as effect sizes (for non-standardized values) with 95% CIs. Bold numbers for significant values, except in intercepts.

	Female	Male
First Line Travel duration (s)	**0.67 (0.68, 0.66)**	**0.79 0.78, 0.80)**
Second Line Travel duration (s)	**-0.77 (-0.76, -0.78)**	**-0.83 (-0.82, -0.84)**
Estimated break point (s)	**19.80 (20.02, 17.60)**	**20.57 (20.24, 20, 91)**

APPENDIX S9: RATIOS BY SECOND ORDER POLYNOMIAL REGRESSION

Table S9: The effect on DCBr (pre-dive duration-based dive cycle ratio) (a), DCAr (post-dive duration based dive cycle ratio) (b) of dive duration, separated by sex for no bottom duration (NBD) and with bottom duration (WBD) dive types. Mixed effect models included identity, location, year and dive date as random effects, which are given as proportions of total variation explained. Fixed effects are given as effect sizes (for non-standardized values) with 95% CIs. Bold numbers for significant values, except in intercepts.

a) Effect of dive durations on DCBr (pre-dive duration based dive cycle ratio)

	Female NBD	Female WBD	Male NBD	Male WBD
Intercept	-0.01 (-0.16, 0.15)	0.82 (0.61, 1.04)	0.62 (0.49, 0.76)	1.01 (0.77, 1.25)
Dive duration (s)	**0.13 (0.12, 0.14)**	**0.07 (0.06, 0.08)**	**0.06 (0.05, 0.06)**	**0.03 (0.02, 0.03)**
Dive duration^2 (s^2)	**-0.0019 (-0.002, -0.0018)**	**-0.0008 (-0.0009, -0.0007)**	**-0.0006 (-0.0006, -0.0005)**	**-0.0003 (-0.0003, -0.0002)**
ID	0.04	0.03	0.03	0.05
Location	0.02	0.04	0.00	0.04
Year	0.00	0.00	0.00	0.01
Dive date	0.01	0.00	0.01	0.01
Residual	0.95	0.93	0.96	0.89

b) Effect of dive durations on DCAr (ratio of post-dive duration based dive cycle)

	Female NBD	Female WBD	Male NBD	Male WBD
Intercept	0.08 (-0.03, 0.20)	1.48 (1.26, 1.70)	0.63 (0.48, 0.80)	1.16 (0.91, 1.39)
Dive duration (s)	**0.13 (0.12, 0.13)**	**0.016 (0.010, 0.022)**	**0.054 (0.050, 0.060)**	**0.021 (0.015, 0.027)**
Dive duration^2 (s^2)	**-0.0018 (-0.0019, -0.0017)**	**-1.12e-5 (-1.11e-5, 7.01e-6)**	**-6.21e-4 (-6.80e-4, -5.61e-4)**	**-2.32e-4 (-2.87e-4, -1.72e-4)**
ID	0.04	0.04	0.03	0.04
Location	0.00	0.05	0.01	0.03
Year	0.00	0.00	0.00	0.00
Dive date	0.00	0.00	0.01	0.01
Residual	0.96	0.91	0.95	0.91

APPENDIX S10: PATH ANALYSIS

Table 10a: The effect of pre-dive duration on log-dive time. Separated by sex for no bottom duration (NBD) and with bottom duration (WBD) dive types. Mixed effect models included identity, location, year and dive date as random effects, which are given as proportions of total variation explained. Fixed effects are given as effect sizes (for non-standardized values) with 95% CIs. Bold numbers for significant values, except in intercepts.

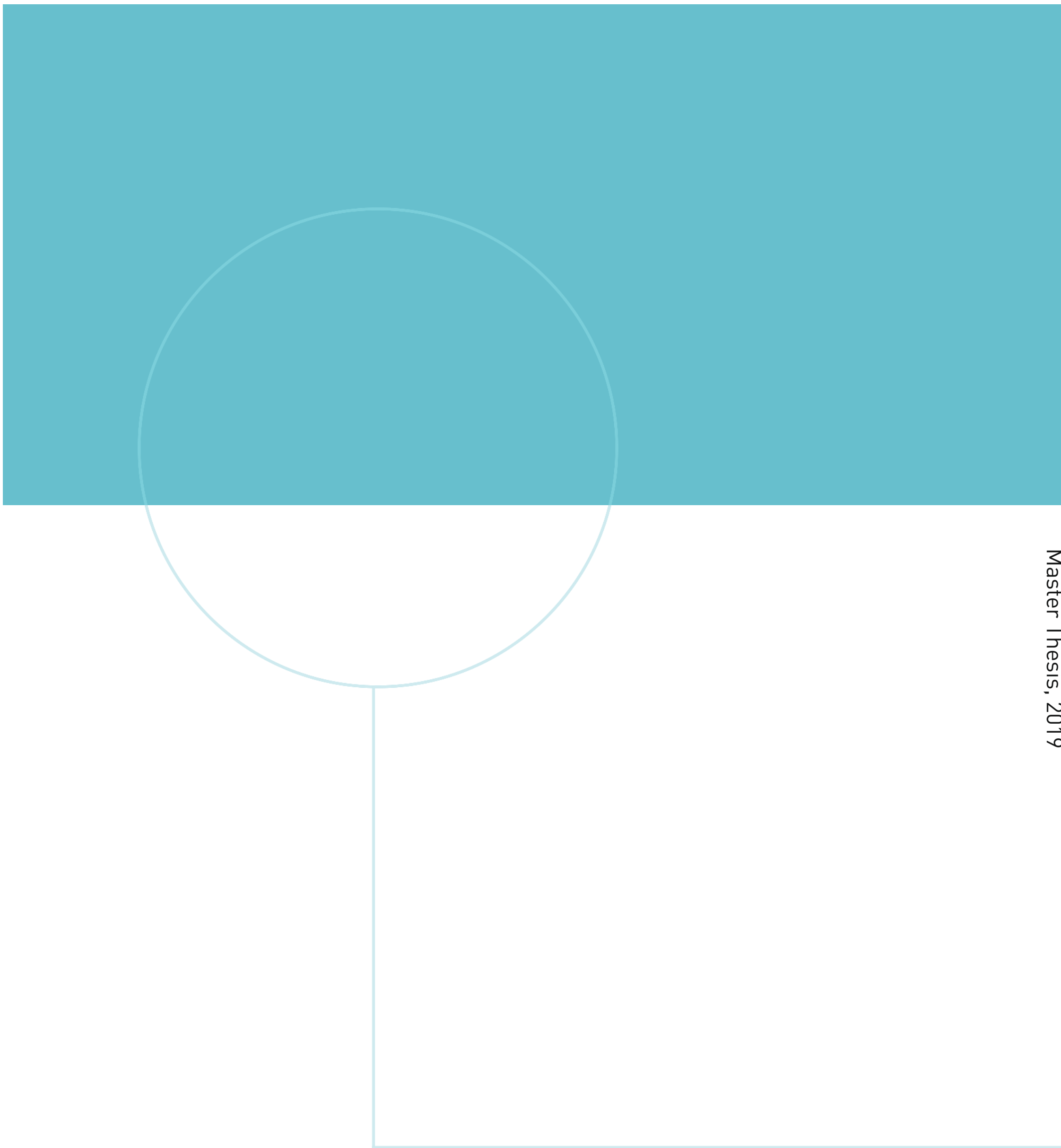
a) The effect of pre-dive duration on log-dive time

	Female NBD	Female WBD	Male NBD	Male WBD
Intercept	2.88 (2.65, 3.11)	3.39 (3.23, 3.44)	3.19 (2.95, 3.44)	3.62 (3.51, 3.73)
Pre- dive duration (s)	-4.43e-4 (-9.42e-4, 8.19e-5)	**2.78e-3** **(2.49e-3, 3.09e-3)**	**2.47e-3** **(2.00e-3, 2.93e-3)**	**2.56e-3** **(2.35e-3, 2.77e-3)**
ID	0.16	0.22	0.10	0.16
Location	0.08	0.14	0.09	0.05
Year	0.00	0.00	0.03	0.01
Dive date	0.05	0.01	0.08	0.13
Residual	0.71	0.63	0.70	0.67

Table S10b: The effect of pre-dive duration and dive duration on log-transformed post-dive duration. Separated by sex for no bottom duration (NBD) and with bottom duration (WBD) dive types. Mixed effect models included identity, location, year and dive date as random effects, which are given as proportions of total variation explained. Fixed effects are given as effect sizes (for non-standardized values) with 95% CIs. Bold numbers for significant values, except in intercepts.

b) The effect of pre-dive duration and dive duration on log-transformed post-dive duration

	Female NBD	Female WBD	Male NBD	Male WBD
Intercept	2.23 (2.15, 2.32)	2.04 (1.93, 2.16)	2.24 (2.15, 2.33)	2.24 (2.12, 2.35)
Dive duration (s)	**1.58e-2** **(1.45e-2, 1.72e-2)**	**2.48e-2** **(2.40e-2, 2.56e-2)**	**2.27e-2** **(2.15e-2, 2.38e-2)**	**2.39e-2** **(2.32e-2, 2.47e-2)**
Pre-dive duration (s)	**4.21e-3** **(3.72e-3, 4.68e-3)**	**2.96e-3** **(2.58e-3, 3.34e-3)**	**3.95e-3** **(3.44e-3, 4.44e-3)**	**2.74e-3** **(2.43e-3, 3.05e-3)**
ID	0.03	0.03	0.02	0.04
Location	0.01	0.10	0.00	0.07
Year	0.00	0.00	0.01	0.00
Dive date	0.01	0.00	0.00	0.01
Residual	0.95	0.87	0.97	0.86



Master Thesis, 2019

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