

## RESEARCH ARTICLE

# Temporal non-independence of foraging dive and surface duration sequences in the European shag *Gulosus aristotelis*

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## Abstract

Studies of foraging behaviour and respiratory physiology in breath-holding divers often assume that each dive cycle (dive plus surface duration) is physiologically and ecologically independent within a series (or “bout”) of sequential dives. We tested this assumption using time depth recorders and GPS data for more than 42,000 dives in 1289 bouts by 39 pairs of male and female European shags (*Gulosus aristotelis*) provisioning nestlings. We found distinct patterns of temporal autocorrelation over several dives within bouts, but this was driven mainly by consecutive dives of the same type, that is, runs of V-shaped (presumably prey searching) versus U-shaped (presumably active hunting) dives. We found no evidence of cumulative physiological effects (i.e. fatigue and/or lowered body temperature) across dives within a bout. However, within-individual variation in dive behaviour revealed complex interactions. Longer bouts were associated with more V-shaped dives, including more and longer runs of V-shaped dives. Meanwhile, more U-shaped dives and longer runs of U-shaped dives acted as limiting factors to bout lengths, with longer bouts being associated with more U-shaped dives only later in the bout. Interactions between bout length and body mass, and between dive order within the bout and body mass, also suggested various size-specific patterns in the temporal distribution of U-shaped dives. Long bouts and bouts ending in longer runs of V-shaped dives were more likely to indicate the termination of foraging activity. However, neither dive type nor bout length predicted whether individuals subsequently (i) stayed to forage in the same location or (ii) moved to a new location to continue foraging within the same trip from the nest. European shags therefore showed temporal non-independence across successive dive cycles and successive bouts of dives, likely as a result of temporal and spatial variation in prey availabilities rather than cumulative physiological effects that might contravene the assumptions in models of optimal dive behaviour.

## KEYWORDS

dive behaviour, dive cycles, foraging behaviour, marginal value theorem, physiological constraints, TDR, telemetry, temporal autocorrelation

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## 1 | INTRODUCTION

When investigating the behavioural and physiological relationship between dive duration and surface duration (before or after a foraging dive) in breath-holding diving vertebrates, each dive cycle is often assumed, for simplicity, to be statistically independent (see Carbone & Houston, 1996; Carlsen et al., 2021; Elliott et al., 2008; Walton et al., 1998; Wilson, 2003). This assumption might be justified for dives with long restitution breaks in between, but high-frequency dives with short surface durations within long bouts or sequences of dives would seem likely to create various types of temporal autocorrelations in dive parameter values across successive dive cycles. Such increased similarity in the characteristics of dives close in time potentially creates a problem of non-independence, and this should be driven by various cumulative physiological or ecological effects (i.e. labelled a–c below).

It is generally assumed that to be able to maintain a high frequency of dives the animal must fully recover on the surface between successive dives. Failure to do so could result in statistical temporal autocorrelations across successive dives due to a build-up of severe and constraining (a) physiological fatigue and/or thermal loss (Leeuw, 1996; Scholander et al., 1950; Williams, 1999). Such effects would ultimately compromise the efficiency of any dive strategy (Carbone & Houston, 1996; Walton et al., 1998). However, cumulative physiological effects of long or demanding dives on subsequent dive cycles have rarely been examined (but see Hart et al., 2010). Even within a sequence of highly time- and energy-efficient dive cycles, we might occasionally expect to see dive strategies that lead to the temporary build-up of cumulative costs. One reason may be that the diving animal experiences (b) changes in the marginal costs/benefits of foraging effort as the collected load size (e.g. stomach contents) increases. Additionally, a trade-off to maximize the immediate opportunities for foraging while mobile prey are present during one or more successive dives is likely to be common. Thus, cumulative physiological effects are not the only potential cause of temporal autocorrelations within a bout of sequential dives. Any autocorrelation could instead be the result of ecological similarities between successive dives close in time and space, with animals employing the same dive-cycle strategy across different dives to search for and gather the same types of prey at the same depths or in the same micro-habitats. Temporal autocorrelation in dive parameters across dives may thus also be a result of (c) cumulative depletion/dispersal of potential prey in the diving location, due to short-term spatio-temporally similar foraging conditions. We now elaborate on each of these three types of effect in turn with their predictions.

When investigating cumulative physiological effects of dives, the recovery time on the surface post-diving is a key parameter due to its reflection of the energetic demands in the previous dive (see Carlsen et al., 2021). During these restitution periods either between dives or between bouts, carbon dioxide (CO<sub>2</sub>) needs to be exhaled (Stephenson et al., 1986) and oxygen (O<sub>2</sub>) loaded up ready for the next dive(s). The uptake rate of O<sub>2</sub> follows diminishing returns and therefore crucially affects optimum surface durations (Carbone

& Houston, 1996; Walton et al., 1998). However, if a subsequent dive is induced before full surface recovery, this may lead to a temporal autocorrelation in dive parameters across longer sequences of dives. This may apply to species hunting elusive fish prey, as the diving animal needs to be underwater for an unpredictable length of time in order to successfully catch prey. Thus, (a) fatigue due to accumulation of CO<sub>2</sub> or lactate, or to not fully restoring O<sub>2</sub> in blood and tissue, could build up over longer sequences of dives or even across bouts of dives (Jones et al., 1988). Build-up of fatigue may ultimately affect not only dive behaviour within the bout, but also subsequent hunting strategies across bouts and when to return to the nests for central-place foragers. Thus, fatigue that extends across dive cycles may be indirectly measurable as systematic changes in dive parameters as a result of the change in time budget during a bout (Carlsen et al., 2021), leading to long-lasting temporal autocorrelation patterns.

Furthermore, foraging trips in many species consist of multiple diving bouts, often at more than one location, before returning to the central place (Houston & McNamara, 1985; Ydenberg & Davies, 2010), meaning that any cumulative physiological effects within a trip could affect the overall time budget of the animal. In addition, successive increases in stomach contents or bill loads towards the end of a bout or trip might increase mass-dependent foraging and flight costs and thus alter the marginal value of different diving strategies across successive dives (Carlsen et al., 2021). Similar to the respiratory arguments above, any decrease in body temperature of a diving animal in cold waters needs to be regained between dives in order to avoid detrimental long-term effects (Grémillet et al., 2001; Scholander et al., 1950). Animals that do not induce the dive response (see Irving et al., 1942) must maintain body temperature during diving bouts through increased metabolic rate while underwater and/or thermal recovery at the surface that both affect the length of surface durations (Enstipp et al., 2005; Leeuw, 1996). In addition, the ingestion of cold prey in a diving seabird has been shown to reduce abdominal temperatures during diving bouts (Kato et al., 1996). Although such a decrease in temperature could mean lowered metabolic rate, an instant heat-up of the ingested food to maintain body temperatures and facilitate any digestion has been shown to instead increase the metabolic rate further (Enstipp et al., 2005). In addition, core body temperatures in seabirds have been shown to increase during dives due to increased muscular activities, while peripheral tissue temperatures decreased so that overall heat loss during dives was limited (Niizuma et al., 2007).

The cumulative and possibly combined effects of (a) respiratory fatigue and increased thermoregulatory costs may result in shorter dive durations with longer corresponding surface durations towards the end of bouts and/or trips. Because foraging trips in many species consist of multiple diving bouts often at many locations before returning to the central place (Houston & McNamara, 1985; Ydenberg & Davies, 2010), dives towards the end of bouts, or even towards the end of foraging trips, could become more costly in terms of cumulative physiological costs and surface recovery times, as compared to early dives. Body size is also expected to influence all these effects

(Carlsen et al., 2021), because larger individuals tend to have greater dive endurance due to greater gas and energetic storage (i.e. glyco-gen access) and lower size-specific metabolism, as well as improved cold tolerance due to a lower surface-to-volume ratio that affects heat capacity (Quillfeldt et al., 2011).

Optimal foraging theory in the form of the Marginal Value Theorem (MVT, Charnov, 1976) has been applied to both individual diving behaviour (Carbone & Houston, 1996; Carlsen et al., 2021; Houston & McNamara, 1985; Stephens et al., 2007; Walton et al., 1998), trip durations and patch residence times in central-place foragers (see Ydenberg & Davies, 2010). Individuals are assumed to optimize their returns from foraging effort by adjusting dive durations or patch residence in the face of escalating costs in energy or recovery times at the surface (Carbone & Houston, 1996; Houston & McNamara, 1985) and/or diminishing benefits in prey availability and loading (Charnov, 1976; Kacelnik, 1984; Nonacs, 2001). These non-linear effects on dive or patch profitability ultimately lead to a point when the forager should quit and switch to a new foraging opportunity in terms of a return to the surface (and a new dive) or a new patch location perhaps via the central place nest or roost (Charnov, 1976; Stephens et al., 2007). In the case of (b) prey loading, greater hunger from parental energetic needs at the beginning of a bout (or trip) may provide steeper self-feeding marginal gains per prey item captured during early compared to later dives (Stephens et al., 2007), leading to temporal autocorrelations due to spatiotemporal similarities among successive dives based upon their proximity within a bout or trip. This might affect optimal dive cycles (dive depths and dive and surface durations) across the length of a bout (or trip), as longer and more costly dives might be more profitable earlier in foraging sequences. Although such a decrease in the marginal value will not affect the value of successive prey gathered for the purposes of provisioning towards the end of a trip, it may affect parental provisioning decisions concerning exactly when to terminate foraging activities.

Foragers tend to experience (c) a gradual prey depletion the more time that they spend foraging at the same patch or location (Charnov, 1976; Stephens et al., 2007). This is likely to be the case for diving animals that hunt elusive pelagic or benthic fish prey, where each dive will involve a trade-off between maintaining efficient dive cycles (Walton et al., 1998) and the benefits of exceeding optimal dive durations in order to catch already detected prey before they are lost. Indeed, the detection of prey (e.g. a school of fish) during a dive may increase the probability of further successful foraging and thus the marginal value of immediately subsequent dives in that location, creating an ecological non-independence across adjacent dive cycles as has been shown in macaroni penguins, *Eudyptes chrysolophus* (Hart et al., 2010). Conversely, the consumption as well as the disturbance and subsequent dispersal of mobile fish prey as a result of active foraging may mean that diving animals experience a cumulative depletion of potential prey (i.e. the MVT “diminishing returns” with patch residence time, see Charnov, 1976; Kacelnik, 1984). Depending upon the prey type and foraging conditions, such prey depletion may happen on different timescales ranging from a single

dive to multiple dives or bouts in a particular patch or location. The spatiotemporal aggregations of prey encounters imply a non-random distribution of hunting versus information sampling dives throughout a bout (Hart et al., 2010). Hence, the type of dive in terms of the depth and duration, and likelihood of V-shaped versus U-shaped dive-depth profiles (see Carlsen et al., 2021), may be predictable based upon the (number and type of) previous dive(s) in the bout.

Therefore, although not formally part of any existing MVT models, the changes in dive costs described in (a), or in benefits described in (b) and (c), would create non-linear effects at intermediate timescales. This could cause temporal autocorrelations in dive-cycle parameters across adjacent dive cycles and/or over a bout, or even across different bouts of dives. Such temporal non-independence contravenes the assumptions of MVT optimality models concerning diving behaviour and central-place foraging and may therefore contribute to a significant change in expectations if they are not taken into account in statistical analyses of dive behaviour. In this paper, we explore various sources of carry-over effects and non-independence of adjacent dives and bouts seen as changes in time budget and foraging pattern in a high-frequency diver, the European shag (*Gulosus aristotelis*, prev. *Phalacrocorax aristotelis*). We investigate temporal autocorrelations in the durations of different components of the dive cycle, the distributions of different types of foraging dives within bouts, and especially any runs in dives of the same type, preceding bout termination and the subsequent choice of the individual to stay, move to a new location or terminate foraging activity. Given the importance of such temporal non-independence for the understanding and interpretation of natural variation in foraging dive cycles, dive locations and bout durations in the behavioural ecology and respiratory physiology literature, we draw specific conclusions regarding such complications for the study of adaptive foraging strategies in breath-holding diving animals.

## 2 | METHODS

### 2.1 | Study site and species

The Sklinna archipelago, situated about 20 km off the coast of Vikna in Trøndelag, Norway (65°12'N 10°59'E), holds one of the largest European shag colonies in Norway, with ~2000 breeding pairs in 2017 (see Carlsen et al., 2021). In this area, 90% of the diet of European shags consisted of 0–2 group gadoid species, dominated by saithe *Pollachius virens* in both numbers, biomass and frequency (Hillersøy & Lorentsen, 2012). The shags seek out flat areas of seabed containing kelp forest, where such pelagic prey are found in shallow waters (Christensen-Dalsgaard et al., 2017).

### 2.2 | Ethical note

Capture and handling of birds were approved by the Norwegian Environment Agency (2013/2306, 2014/2179, 2015/3042, 2016/

3366, 2017/4069, 2018/607) and the Norwegian Animal Research Authority (5148–2013/34672 (2013e2015), 7484–2015/55385 (2015e2017), 12,163–2017/67495 (2017e2019)). All handling of birds was done by Felasa C approved persons, or under supervision of such persons. The authors have no conflict of interest.

### 2.3 | Data collection

As in the study by Carlsen et al. (2021), the fieldwork took place during June–July 2013–2018 and included 78 birds (39 pairs) over six different breeding seasons. Chick-rearing shags were chosen based on their nest accessibility and how “protective” the pairs were, as those that aggressively stayed around the nest were easier to capture/recapture. Parental birds were fitted with loggers when nestlings were approximately 5–35 days old. Nestling age was determined using morphological criteria determined from control nests within the same colony that were checked every fifth day. The shags were captured and then recaptured at their nest by hand or using snares. Each individual was fitted with a GPS logger (i-gotU GT-120, Mobile Action Technology, New Taipei City, Taiwan; refitted in heat-shrink tubes) and a time depth recorder (TDR, G5, CEFAS Technology Ltd, Lowestoft, U.K.). TDR loggers were attached to the GPS loggers prior to instrumentation, and the loggers were attached to three to four middle tail feathers using TESA tape. The maximum logger deployment weight was 30.6 g, corresponding to 1.6% and 1.8% of mean body mass of males and females, respectively. The GPS loggers recorded location ( $\pm 10$  m) every 30 s, and the TDR recorded depth ( $\pm 0.1$  m) every 1 s. The loggers were removed during recapture after approximately 2–5 days. Deployment of loggers normally required less than 3 min of handling and retrieval less than 10 min, and no harmful long-term disturbance effects were noted in either adults or their chicks.

The sex of adults was determined initially by body size features and ultimately via their vocalizations (Cramp & Simmons, 1977), because males and females made very distinct types of calls while defending the nest at our approach (Snow, 1960). At first capture, body mass was obtained using a Pesola spring balance (accuracy  $\pm 10$  g). Both adults in the pair were fitted with recording instruments during the same breeding season, although not overlapping in time but usually within only a few days of each other. At recapture, wing length (ruler  $\pm 1$  mm), head and bill length (digital calliper  $\pm 1$  mm) and body mass (see above) were obtained. Adult female average mass was 1610 g (range 1370–1860 g), while average adult male mass was 1920 g (range 1660–2280 g). Growth data (i.e. capture–recapture difference in chick weight) were collected for all nests and these measurements were compared to a control area within the same colony containing 50 nests where adults were not fitted with loggers. There was no indication of parents reducing their provisioning rates or changing any patterns of nestling feeding for any birds included in this dataset. There were no obvious differences in the number of surviving chicks in experimental versus neighbouring control nests, aside from impeded survival due to gull predation.

### 2.4 | Data handling

Data handling and simulations were conducted with software R (R Core Team, 2018).

For the dive data, similar to Carlsen et al. (2021), the TDR raw data files were calibrated and summarized using the library dive-Move (Luque, 2007). The dive threshold was set to 1 m (i.e. shallower dives were not included). The zoc method (Luque, 2007) was used for calibrating depth with three sequential filters: an initial median smoothing filter with 3 s window width, followed by a 0.1 quantile filter with 3 s window width and ending with a 0.02 quantile filter with 60 s window width. The process was bound to depths between  $-4$  and 4 m. For each dive, depth and duration were calculated (see Appendix S1). Dives with a depth change rate of  $\geq 3$   $\text{m s}^{-1}$  were regarded as unlikely (Watanuki et al., 2008) and removed from the dataset.

The total number of dives in this study was 42,014 after data selection, but with smaller subsamples used for some of the analysis (given below and in table texts). Dives were classified into two types according to the presence/absence of a horizontal dive bottom duration: U-shaped (with a horizontal dive bottom component) versus V-shaped (with no horizontal dive bottom component) dives (See Appendix S2), and these are assumed to represent active hunting dives involving possible prey captures versus prey search/sampling dives likely involving no prey captures, respectively (see Appendix S3). V-shaped dives were on average shallower and shorter in duration than U-shaped dives, and the durations of both had positive non-linear effects on the subsequent surface (recovery) durations, although the effect of U-shaped dive durations on such recovery was significantly stronger than of V-shaped dives (Carlsen et al., 2021). The depth change rate (m/s) during descent was on average higher in U-shaped dives versus V-shaped dives (see example in Appendix S2).

Post-dive durations at the surface longer than 360 s were used to separate dives into dive bouts (i.e. distinct sequences of successive dives at one location) as surface durations longer than this could not be explained by simple replenishment of  $\text{O}_2$  storage or momentary resting within a dive bout. Model parameters used in this paper are summarized in Table 1. The spatial locations of dives were determined by relating each dive to the GPS position closest in time, restricted to maximum 30 s difference between the time of the GPS position and the time when the dive began or ended. This cut-off was applied to compensate for the fact that GPS devices did not record positions when submerged while still retaining a high spatial resolution in the data. GPS data were processed using R library ggmap (Kahle & Wickham, 2013) to qualitatively identify a total of 23 distinct foraging locations (see Appendix S4) based upon where most of the dives occurred (i.e. clusters of dives surrounded by areas with no dives). In particular two larger clusters of dives were closely examined before being split into two lots of two different locations, based upon the large differences in depth within the cluster (see example in Appendix S4) as determined from a topographical base map by Kystverket (<https://kart.kystverket.no/>), as sea

**TABLE 1** Description of the dive parameters derived mainly from GPS, TRD and demographic data.

Parameter	Description
<i>Maximum depth</i>	The deepest vertical distance from surface in meters per dive.
<i>Descent duration</i>	Time spent in vertical movement descending.
<i>Bottom duration</i>	Time spent in horizontal movement per dive.
<i>Ascent duration</i>	Time spent in vertical movement ascending.
<i>Post-dive duration</i>	Time spent on the surface after each dive, up to 360 s.
<i>Dive number</i>	The consecutive number for each dive within a <i>bout</i> , which was log transformed absolute bout length for all analyses to control for differences in <i>bout length</i> .
<i>Bout</i>	A sequence of consecutive dives by the same individual, separated by between dive durations of >360s (see methods).
<i>Bout ID</i>	Factorial label for each bout, for identifying dives that belong to the same bout.
<i>Bout length</i>	The number of consecutive dives in a bout.
<i>V-shaped dives</i>	Dives with no <i>bottom duration</i> , assumed to be information sampling dives involving searching for prey but no active foraging. Binomial value 0.
<i>U-shaped dives</i>	Dives with <i>bottom duration</i> , assumed to be hunting dives involving active pursuit of prey. Binomial value 1.
<i>Dive type</i>	<i>V-shaped dives</i> or <i>U-shaped dives</i> .
<i>Runs of dive type</i>	Multiple adjacent dives in a sequence within a bout that are strictly of the same <i>dive type</i> .
<i>Year</i>	Identifier for the 6 years from 2013 to 2018.
<i>IndividualID</i>	Individual identity by ring number.
<i>Location</i>	Label for the 24 different locations determined from clusters of dives.
<i>Day</i>	Day of the year (i.e. from 1 to 365), to reflect seasonal variation.

depth is an important predictor of habitats selected during foraging (Christensen-Dalsgaard et al., 2017).

## 2.5 | Statistical analyses

All statistical analyses were performed using R (R Core Team, 2018/2019). To test for any temporal autocorrelations (TAC) in the dive parameters, first within bouts and then runs of dive types

(a total of 18,923 runs), we used the “acf”-function in the “nlme” packages (Pinheiro et al., 2020), producing correlogram figures and tables of correlation values per time lag for dives within a bout (i.e. the number of the dive in the correct order within a bout). The dive cycle parameter response variables (i.e. maximum depth, descent duration, bottom duration, ascent duration and post-dive surface duration) in the temporal autocorrelation tests were log-transformed prior to analysis to normalize residuals, ensuring mostly simple linear effects (i.e. for any of the expected exponential progressions) and models with non-normally distributed response variables (i.e. bout lengths and run lengths) were variance standardized to allow easier comparison across effect sizes of different variables. The random effects in the models were: year, day, foraging location, identity of the bird and dive bout. Fisher's Z-values were used to calculate confidence intervals (CI's) via the “qnorm” function, with alpha quantiles of 0.05. When testing for temporal autocorrelations, the identity of each bout within the identity of each bird was included as a random effect. The level of autocorrelation at each lag number ( $t + 1$ ,  $t + 2$ ...,  $t + n$ ) was set to the number of a dive within the given bout or sequence (“run”) of dives with the same divetype. In the corrected models, the respective dive parameter value for the previous dive was included as a fixed effect along with the previous dive type. Note that in the AFC results, after all corrections have been made, there was often a very small but significant negative temporal autocorrelation, especially for U-shaped dive parameters. This happens due to the rather small CI's of the models as a result of the large dataset, plus the extensive corrections produced by the individual runs (e.g. Table S5) and the previous-dive parameter values, resulting in a slightly over-fitted model. Although not ideal, this should still be considered better than leaving the correction parameters out completely. Similarly, the occasional negative dip in the autocorrelated effect of the  $t_{-1}$  value is a result of this overfitting, because by including the parameter of the previous dive we are specifically over-correcting for  $t_{-1}$  effects. However, the effect sizes involved here are still minimal (see Results), and the previous dives parameter (i.e.  $t_{-1}$ ) is the main parameter correcting for the correlation between  $t_{-0}$  and  $t_{-2}$ ,  $t_{-3}$ , and so on, and is therefore very important to include.

Among- and within-individual effects were explored using the mean and mean-centring dive parameter values, respectively, for each individual (see Carlsen et al., 2021; Van De Pol & Wright, 2009). Among-individual effects were derived using individual averages ( $n = 78$ ) and analysed with the only random effect in the models therefore being year. Within-individual effects were derived from mean-centring of dive parameter values for each individual ( $n = 42,014$ ), and all original random effects could therefore be included in the models. Body mass was included in models instead of sex to test for size-specific variation among individuals although the species shows strong sex dimorphic traits. This is based on the findings in Carlsen et al. (2021), showing an almost complete overlap between the statistical effects of sex and body mass in this same dataset.

Generalized mixed-effect models (GLMER) for binary distributed data were used to analyse parameters influence on the probability



of the type of dive (V-shaped [0] versus U-shaped dives [1]), with the package "lme4" (Bates et al., 2015).

Post-bout behaviour was divided into: (i) stay and forage in the same location, (ii) move to forage in a new location or (iii) termination of foraging activity. The dive bout characteristics associated with these outcomes were tested using mixed-effect models, with Helmert's contrasts providing the required comparisons. The definition for termination to foraging activity was set to a time limit of 3600s (1 h) between successive dives, interpreted as a change in activity. Post-bout behaviour was then used as a categorical predictor for different variables relating to bouts and the dives they contained. First, we tested for differences in the dives in the last part of each bout, such as final run length (of consecutive dives strictly of the same type) and the last dive type. Second, we looked for differences in variables describing features of the bout, such as average dive type and bout length. The number of observations in this analysis was equal to the number of bouts involving more than 5 dives ( $n = 931$ ), divided into number of bouts ending with V-shaped dives ( $n = 375$ ) versus the number of bouts ending with U-shaped dives ( $n = 556$ ). All dives that terminated a bout are depicted on a map within their respective location in Appendix S6.

Estimated effect sizes are given as  $\pm 95\%$  confidence intervals (CI), and random effects are presented as proportions of random variation explained. Marginal  $R^2$  values are given for proportion variance explained by both the fixed effects and random effect structure. Akaike information criterion (AIC) values and  $p$ -values were used for model selection to decide upon the inclusion/exclusion of all fixed effects and of non-linear (i.e. squared) terms and interaction terms (see Forstmeier & Schielzeth, 2011); full model selection procedures for fixed effects are presented in Appendix S7. Residual distributions for all models were checked for normality of data using qqplot (Becker et al., 1988). Potential correlations between covariates in the models were assessed using Variation Inflation Factors (VIF), within package "olsrr" (Hebbali, 2020), and correlated explanatory variables were not included in the same model. Dive bouts with less than 5 dives were excluded in order to properly test for effects due to sequential dives, with all data selection resulting in a full size dataset with 42,014 observations.

## 3 | RESULTS

### 3.1 | Temporal autocorrelations in dive parameters across successive dives

Using the sequence of dives per bout, including both V-shaped and U-shaped dive types, temporal autocorrelations over a range of time lags were visible for the all dive cycle parameters (Figure 1). The uncorrected correlograms (Figure 1, top panel) show a positive but decreasing level of temporal autocorrelation up to a maximum lag of 5 to 10 successive dives (Table S5). After this, there was rarely any clear or consistent pattern of autocorrelation among adjacent dives. However, this pattern changed completely when correcting for the

parameter value of the previous dive, with almost all the temporal autocorrelation between dives (beyond two directly adjacent dives) disappearing ( $<5\%$  correlation from 1st lag, Table S5).

### 3.2 | Consecutive runs of V-shaped or U-shaped dive types

The temporal autocorrelations above over mostly only one dive (Figure 1 and Table S5) did not control for dive type of successive dives. Given that dive parameter values differ systematically according to dive type (Carlsen et al., 2021), it is possible that any temporal autocorrelation here was simply due to the temporal clustering of dives of the same types within a bout (i.e. runs of V-shaped or U-shaped dives). Therefore, we tested for such temporal clustering for both dive types (see Figure S8). To avoid confounded results, the data were decomposed into within- and among-individual effects (Carlsen et al., 2021; Van De Pol & Wright, 2009), where the less relevant non-decomposed and among-individual effects are given in Table S8.

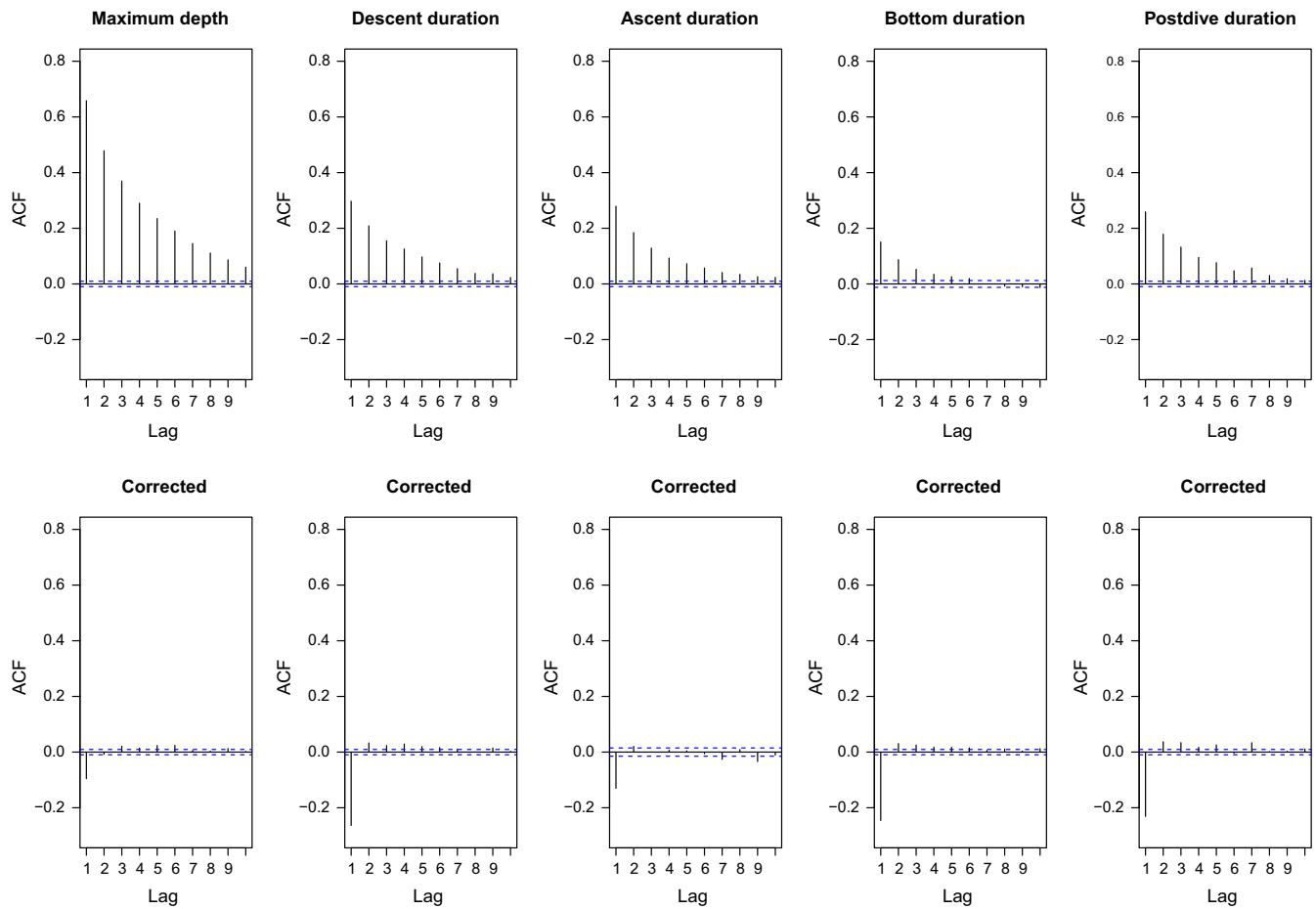
Within individuals, the length of consecutive V-shaped dive runs increased with the relative length of the bout (Table 2). Runs of U-shaped dives increased with dive number and decreased with bout length, with a negative interaction between the two variables (Table 2). This means that relatively longer runs of U-shaped dives towards the end of bouts occurred more often in relatively shorter bouts, resulting in bouts (and perhaps trips) being ended (see below).

### 3.3 | Temporal autocorrelations within runs of V-shaped and U-shaped dive types

In the light of the results above regarding runs of the same dive type, we then analysed the temporal autocorrelations for all dive parameters, but this time within those continuous runs or sequences of dives of the same type (i.e. V-shaped or U-shaped dives). We found that all temporal autocorrelations substantially decreased (Figures 2 and 3, Table S9) compared to the dive bout analyses (Figure 1, Table S5), confirming that almost all the previous covariance across adjacent dives was due to runs of the same dive type.

### 3.4 | Changes in frequency of dive type and runs of dive type throughout a bout

The dive type (V-shaped versus U-shaped dives) of any one dive was explained in the original data set by a model involving dive number, previous dive type and an interaction between the two, as well as effects of bout length and body mass, and an interaction between body mass and previous dive type (Table S11). One reason for this complexity is, again, that these analyses confound within- versus among-individual variation in dive behaviour (see Carlsen et al., 2021; Van De Pol & Wright, 2009). By decomposing the data into explanatory variables containing either within- or



**FIGURE 1** Correlograms for temporal autocorrelation (ACF) across dives with increasing lag (i.e. number of successive dives) for: maximum depth, descent duration, bottom duration, ascent duration and post-dive duration. Results are shown for uncorrected models (top panel) and corrected models, where the dive parameter value during the previous dive (i.e. controlling for  $t_{-1}$  effects) is taken into account. Solid vertical black lines show the level of autocorrelation, with  $\pm$  CIs shown as blue dotted lines, and vertical lines above or below this indicate a significant autocorrelation – see [Table S5](#) for extended dive sequences, more details and statistical estimates. Only the first 10 dives in a sequence were included in the correlogram as this was, in general, how far any consistent patterns of temporal autocorrelation lasted. Number of observations ( $n$ ) was 42,014 dives.

among-individual variation, we could both simplify these model structures ([Table S7](#)) and better explain variation in dive type across dives within individuals ([Table 3](#)) as well as variation across different individuals ([Table S11](#)).

As expected from the analyses above, within-individuals both V-shaped and U-shaped dives were more likely to be preceded by a dive of the same type ([Table 3](#)). As with the temporal autocorrelation effects above, this effect was only detected for the previous dive ( $t-1$ ) type, but not for dives preceding this (i.e.  $t-2$  or  $t-3$ ) in the sequence of dives within a bout ([Table S10](#)). However, this temporal autocorrelation in dive type going back only one previous dive did mean that, by chance, there were quite long runs of consecutive dives of the same type ([Figure S8](#)), which is what allowed the analyses of different run lengths in [Table 2](#). The effect of previous dive type on the current dive type confirms the temporal autocorrelation results (above) and the finding of runs of dives of the same dive type driven by simple  $t_{-1}$  effects.

The among-individual analyses show that the probability of a U-shaped dive decreased as individual body mass and mean individual

bout length increased, although with a positive interaction ([Table 3](#)). This suggests that it was especially larger (male) individuals that extended the length of bouts with runs of V-shaped dives, perhaps when they spent more time searching for prey, mirroring the results above for within-individual effects in [Table 2](#). However, it should be noted that in general longer bout lengths were associated with lighter (female) individuals ([Figure S12](#)), with such individuals completing more but shallower dives per bout in the same location compared to heavier (male) individuals that dive deeper but fewer times per bout (Carlsen et al., 2021).

### 3.5 | Cumulative effects on dive parameters during bouts

We then explored the within-bout effects of dive number and bout length on the various dive parameters and in this case concentrating on only the more revealing within-individual cumulative effects

**TABLE 2** Mixed-effect model results for within-individual effects explaining variation in run lengths (n dives), conducted separately for the two dive types: “V-shaped” dives with no bottom duration ( $n = 16.283$ ) and “U-shaped” with bottom duration ( $n = 25.731$ ), based on the top ranked model using AIC.

Run length	V-shaped dives	U-shaped dives
Intercept	-0.16 (-0.21, -0.11)	0.21 (0.14, 0.27)
Dive no		<b>0.030 (0.014, 0.047)</b>
Bout length	<b>0.056 (0.040, 0.072)</b>	<b>-0.11 (-0.15, -0.07)</b>
Dive no. * Bout length		<b>-0.073 (-0.089, -0.057)</b>
IndividualID	0.04	0.08
BoutID	0.06	0.13
Location	0.01	0.02
Residual	0.89	0.77
R <sup>2</sup> fixed	0.01	0.01
R <sup>2</sup> Random	0.11	0.10
R <sup>2</sup> Residual	0.88	0.89

Note: Effect sizes are given with  $\pm 95\%$  CIs in parentheses, with bold values being significantly different from zero. Asterisk (\*) symbolizes interactions. Random effects of individualID, boutID and location are given as proportions of variation explained. See Table S7 for full models and model selection results and Table S8 for full non-decomposed results and decomposed among-individual results.

within bouts. However, model results for the full undecomposed data set and the among-individual variation are also given in the Tables S13 and S14.

Maximum depth and descent duration in V-shaped dives increased with dive number within bouts (Table 4a), an effect that was less pronounced in longer bouts. Ascent durations showed this same interaction, but without significant main effects. Surface durations following V-shaped dives decreased with bout length, reflecting the reduced costs of shallower depths and shorter dive durations during longer bouts, but there were no corresponding recovery effects on post-dive surface durations of the longer deeper V-shaped dives with dive number.

During U-shaped dives, all dive parameters decreased by increasing dive number within the bout, but increased with bout length (Table 4b). This appears opposite to the effects in V-shaped dives (Table 4a), suggesting less intensive U-shaped dives later in bouts. Body mass interacted positively with dive number, with larger individuals showing less of a decrease in depth and duration of U-shaped dives later in the bouts. Body mass interacted negatively with bout length, with larger individuals showing less of an increase in average depth and duration of U-shaped dives for longer bouts. Individuals of greater body mass perform fewer dives per bout (Figure S12), probably due to each dive by heavier individuals in this same data set being deeper and longer and requiring longer surface durations to recover (see also Carlsen et al., 2021). However, such effects were not apparent in the among-individual models (Table S11), where body mass only seemed to interact with dive number and bout length. The within-individual variation in dive

parameters thus showed complex effects of the dive number within a bout and the absolute bout length, which were neatly mirrored in opposite effects for V-shaped versus U-shaped dives (i.e. V-shaped dives: dive number increase and bout length decrease but with a negative interaction; U-shaped dives: dive number decrease, bout length increase). The interactions with body mass further suggest some logic to this complexity, which might be connected to the temporal patterns of foraging within bouts by shags of different body sizes. It should, however, be noted that the amount of variance explained by all of these fixed effects in this analysis was quite low (<5%), as might be expected from previous analyses of dive-cycle parameters in this same data set (see Carlsen et al., 2021). The size of any dive order effects explained by dive number and bout length interacting with the small amount of variation in body mass here should therefore be relatively small dive-to-dive, but may still be of biological significance over the course of long bouts.

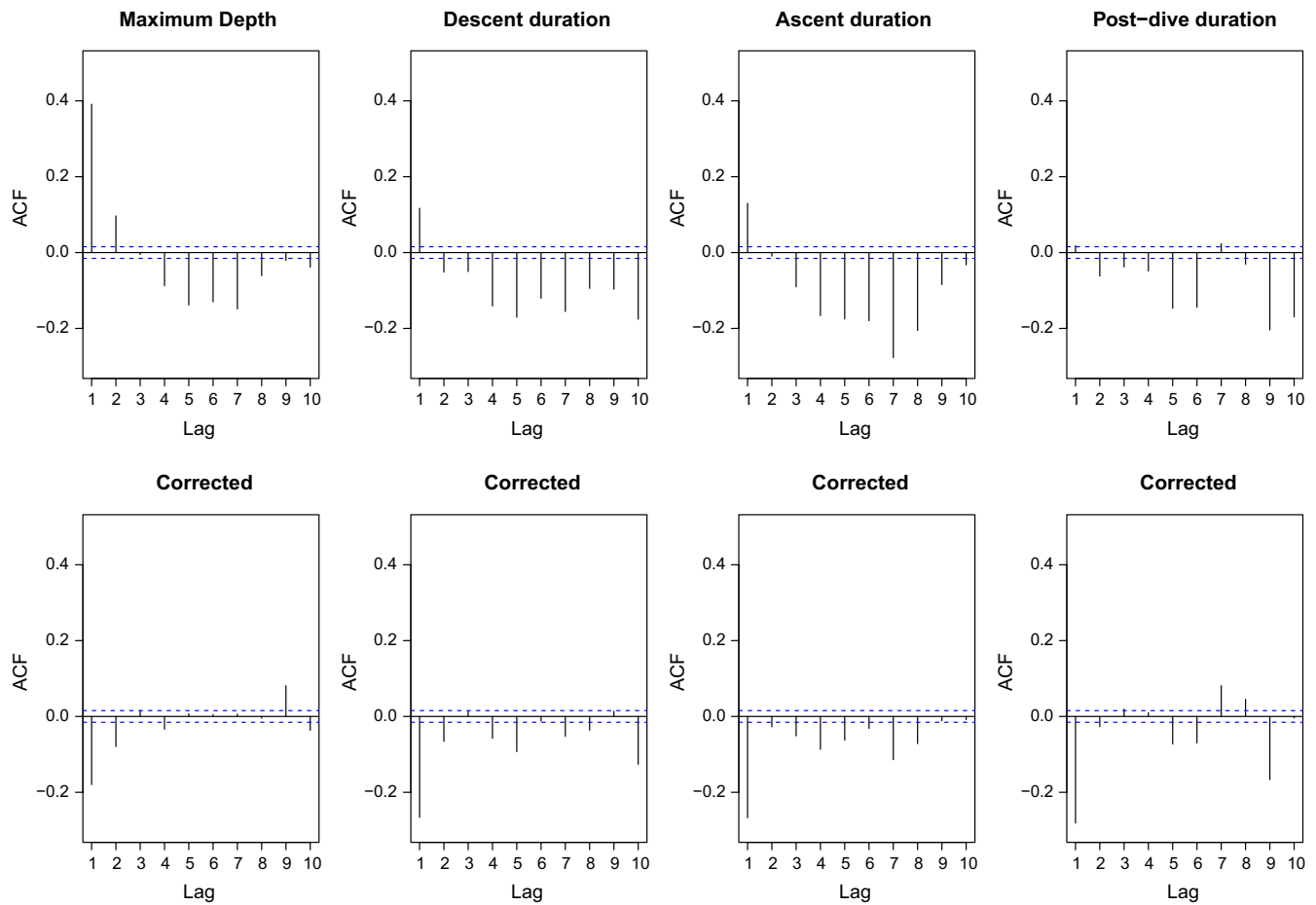
### 3.6 | Bout and patch termination and the temporal distribution of dive types

Finally, it is of interest to ask why diving bouts were terminated, and whether diving behaviour directly before bout termination connects to adaptive decision-making of overall foraging activity, such as moving to a new foraging location or terminating foraging activity altogether. There was no significant difference in final dive type (V-shaped versus U-shaped dives) for bouts that ended with individuals “staying” to forage in the same location, moving to a “new patch” location to forage, or terminating foraging (Table 5). However, bouts that were followed by termination ended with significantly longer runs of V-shaped dives, as compared to bouts that ended with a continuation of foraging in the same location or moving to a new patch. However, the run lengths of U-shaped dives at the end of bouts did not seem to affect the post-bout behaviour. Bouts involving more dives in total were more likely to end with termination of the foraging activity (Table 5; Figure 4), which may reflect an extra final effort put in to foraging within the same location before returning to the nest, rather than paying the cost of pausing to start a new bout or moving to a new foraging location.

## 4 | DISCUSSION

The apparent temporal autocorrelations we initially observed in dive cycle parameters across consecutive dives within bouts were driven almost completely by the non-independence of consecutive dives of the same dive type (i.e. “sampling” no bottom duration V-shaped dives versus “hunting” with bottom duration U-shaped dives). Because U-shaped dives on average were deeper and longer and required longer surface recovery times compared to V-shaped dives (see Carlsen et al., 2021), the non-independence of adjacent dive types caused temporal autocorrelations in all dive parameters. This temporal autocorrelation could therefore be controlled for using the





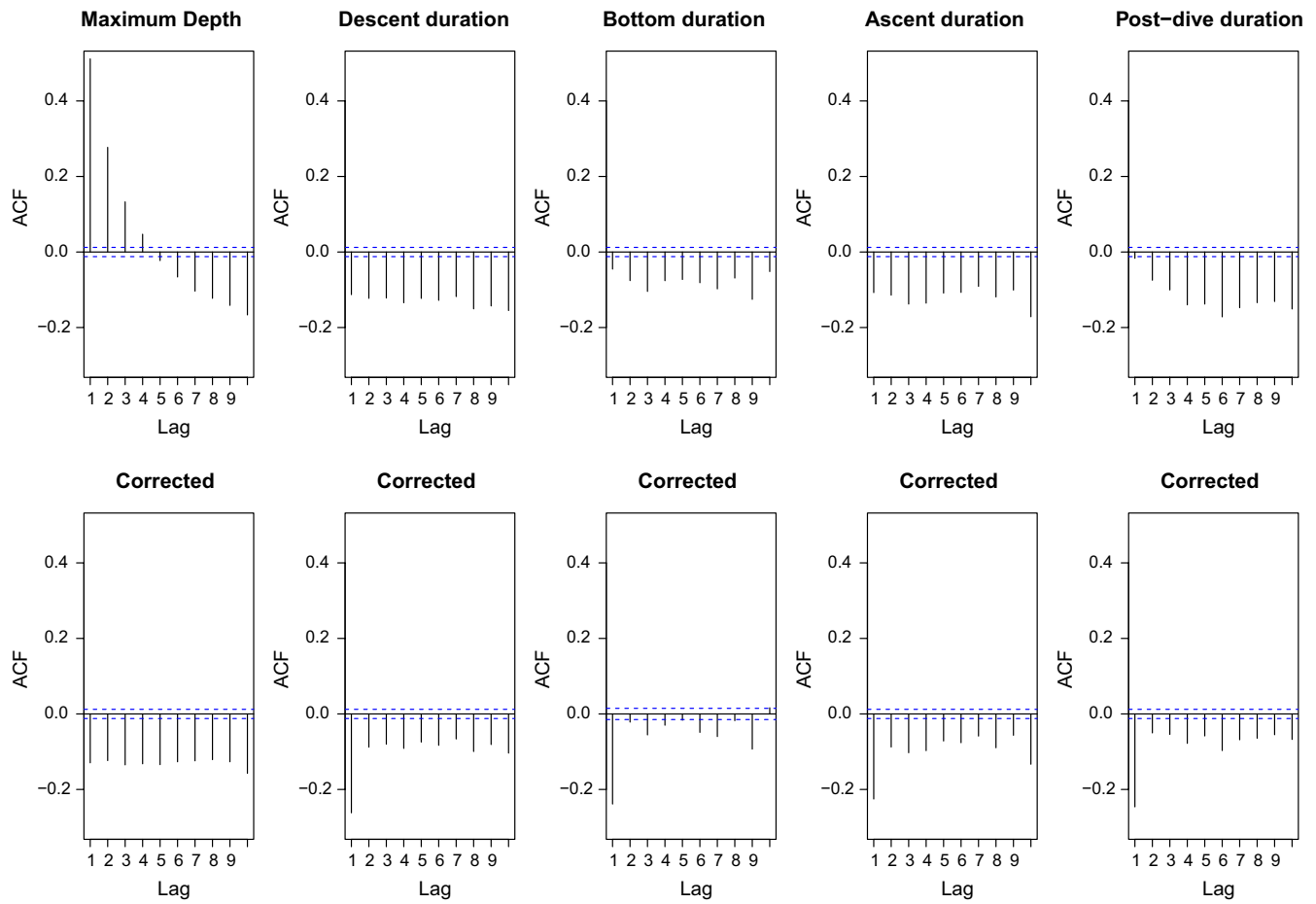
**FIGURE 2** Correlograms for temporal autocorrelation (ACF) effects within runID for V-shaped dives ( $n = 16,283$ ) with increasing lag (i.e. number of successive dives): post-dive surface duration, descent duration, bottom duration, ascent duration and depth. Results are shown for uncorrected models and below each of them their corrected models, which take into account the dive parameter value during the previous dive (i.e. controlling for  $t_{-1}$  effects). Solid vertical black lines show the level of autocorrelation, with  $\pm$ CI's shown as blue dotted lines – see [Table S9](#) for extended dive sequences, more details and [Table S10](#) for statistical estimates. Only the first 10 dives in a sequence were included in the correlogram as this was, in general, how far any consistent pattern of temporal autocorrelation lasted.

dive parameter value of the previous dive and/or the previous dive type, as this corrects for similarities due to dive type-specific costs and similarities in dives due to location-specific traits.

Dive number and bout length were associated with within-bout patterns in dive type, length of runs of the same dive type and any remaining residual variation in the dive parameters (i.e. depth and duration of a dive). This means that dives were also non-independent due to their position in the overall order of dives within bouts of different lengths. The main reason for these temporal within-bout effects in shags seems to be systematic shifts in depths and duration of dives of both dive types during bouts. These effects were most likely caused by changes in dive strategies (i.e. in response to the marginal cost/benefit of foraging dives) and systematic variation in foraging success rates over the course of a bout, leading to the final post-bout decision to stay, move or return to the nest.

We detected no consistent signs of cumulative effects of energetic fatigue and/or lowered body temperatures within bouts, with any remaining temporal autocorrelation effect sizes across dive cycles being so low as to have relatively little biological significance

(i.e. <5%). This finding was confirmed by the fact that increasing dive number within a bout had a positive effect on V-shaped dive depth and descent duration, with no corresponding effect on subsequent surface durations, with these dives notably increasing in frequency with dive number in longer bouts. If there were any effects of fatigue, etc., then they should have been visible as relatively shorter shallower dives accompanied by longer surface restitution durations later in the bout, especially following longer sequences of deeper U-shaped dives from earlier in the bout. Instead, we observed a negative effect of dive number within the bout on both dive durations and corresponding surface duration. Furthermore, lowered body temperatures are assumed to lead to more shallow dives to keep as much as possible of the plumage air layer intact (Grémillet et al., 2005), especially during V-shaped dives where no prey are assumed to be pursued, but there was no sign of such patterns. An increased metabolism due to intensified thermoregulation (Enstipp et al., 2005) should also lead to longer surface duration per dive duration, but no such effects were detected. All of which suggests that the assumption of consecutive dive cycle independence in behavioural



**FIGURE 3** Correlograms for temporal autocorrelation (ACF) effects within runID for U-shaped dives ( $n = 25,731$ ) with increasing lag (i.e. number of successive dives): post-dive surface duration, descent duration, bottom duration, ascent duration and depth. Results are shown for uncorrected models and below each of them their corrected models, which take into account the dive parameter value during the previous dive (i.e. controlling for  $t_{-1}$  effects). Solid vertical black lines show the level of autocorrelation, with  $\pm$ CI's shown as blue dotted lines – see [Table S9](#) for extended dive sequences, more details and statistical estimates. Only the first 10 dives in a sequence were included in the correlogram as this was, in general, how far any consistent pattern of temporal autocorrelation lasted.

and physiological studies may be largely justified (see Carbone & Houston, 1996; Carlsen et al., 2021; Elliott et al., 2008; Walton et al., 1998; Wilson, 2003, among many others), although controlling for possible additional effects on dive-cycle parameters across adjacent dives within bouts or trips is to be recommended. Each separate foraging dive cycle in shags does appear to be self-contained to a large extent in that it includes a sufficient full recovery surface duration to pay for the physiological costs of the previous dive (Carlsen et al., 2021). There is therefore a strong reason to believe that shags constantly regulate their surface durations in accordance with what is needed for full recovery after the dive. Thus, it is the clustering of runs of dives of the same dive type that seems to have caused most of the non-independence effects across adjacent dives, and not as a result of any cumulative (i.e. physiological) effects, but rather more likely due to repeated foraging dives when searching for and predated upon occasional schools of potential prey.

The temporal autocorrelations due to dive type across all variables in the analyses here provide some insight into the foraging behaviour of diving shag at our study site, because there was a clear

distinction between what was important in V-shaped dives versus U-shaped dives, as well as how such effects then co-varied with the order of dives within a bout. When repeatedly diving to the same depth to pursue what we assume must have been the same school of fish prey, maximizing the dive-to-surface duration ratio to more-or-less the same degree would have been key to maximizing efficiency while prey was present (Carbone & Houston, 1996; Walton et al., 1998). This will have produced dive parameters within each run of consecutive U-shaped “hunting” dives that were very similar in depth, length and surface recovery. V-shaped “sampling” dives, on the other hand, were more likely to vary between consecutive dives or different runs of the same dive type, which makes sense if a shag needed to dive to different depths and/or places (e.g. more or less close to shore or within kelp forest stands) to search for schooling prey.

Having said this, the division of dives into only two categories of U- versus V-shaped dive types, and their inferred behaviours of “active hunting” versus “searching” are perhaps an oversimplification of the real foraging dive situation (Cook et al., 2012; Wilson

**TABLE 3** Final mixed-effect model results after model selection for the effect on the probability of dive type (with bottom duration “U-shaped” dives = 1 versus no bottom duration “V-shaped” dives = 0) of various fixed effects and significant interactions for (a) within-individual ( $n = 42,014$ ) and (b) among-individual ( $n = 78$ ) decomposed data.

(a)	Dive type within-individual
Intercept Within-ID	-4.93 e-2 (-6.95 e-2, -2.94 e-2)
Previous dive type	<b>9.23 e-2 (8.27 e-2, 0.10)</b>
BoutID	0.03
Location	0.00
Residual	0.97
R <sup>2</sup> fixed	0.33
R <sup>2</sup> Random	0.00
R <sup>2</sup> Residual	0.66
(b)	Dive type among-individual
Intercept Among-ID	24.20 (12.30, 36.09)
Bout length	<b>-6.39 (-9.35, -3.42)</b>
Body mass	<b>-3.15 (-4.74, -1.55)</b>
Bout length*mass	<b>0.85 (0.45, 1.25)</b>
Year	0.00
Residual	1.00
R <sup>2</sup> fixed	0.33
R <sup>2</sup> Random	0.00
R <sup>2</sup> Residual	0.66

Note: Probabilities are given  $\pm 95\%$  CIs in parentheses, and bold values being significantly different from zero. Random effects of year, bout ID and location are given as proportions of total variation explained. Full models and model selection are given in Tables S7, and S11 gives full undecomposed data results.

et al., 1996), and so there is potential here for more detailed investigations into shag foraging. For example, we do not know whether V-shaped dives always result in no ingestion of prey, or if U-shaped dives always involved one or more prey captures. However, the assumption here of the different types of foraging behaviours occurring within each dive types seems justified based upon all of the information we have here regarding patterns in dive-cycle parameters within and between bouts and the expectation of adaptive time budgeting by individuals (also see Carlsen et al., 2021). Since this population of shags mainly forages on a few, and typically pelagic, fish species over the breeding season (see Methods), there is little reason to believe that different V- versus U-shaped dive types were a result of prey-type-specific hunting tactics (i.e. benthic versus pelagic), as might be likely in other populations of European shags (Grémillet et al., 1998) or different seabird species (Simeone & Wilson, 2003).

V-shaped dive-cycle parameters were more similar within a run of sequential dives than across runs. While U-shaped “hunting” dives should be affected by local prey movements, V-shaped “sampling” dives should perhaps be more standardized within an area, reflecting more the characteristics of local foraging microhabitats (e.g. kelp forest density and depth), which presumably varies

less within than across foraging locations used by the shags. Run lengths of V-shaped “sampling” dives co-varied with the length of bouts and thus reflected possible moves to alternative foraging patches (within or between our “locations”), probably because the frequency of V-shaped dives provided shags with reliable information regarding patch depletion (Stephens et al., 2007; Stephens & Charnov, 1982). In contrast, a given number of successful U-shaped dives were expected to occur before the storage space in the stomach was filled and the foraging activity needed to be terminated. Thus, the number of U-shaped dives is expected to be quite similar among trips that result in sufficient gain (assuming similar biomass of prey success in all U-shaped dives), while the number of V-shaped dives may have no definite limit. Such analyses of these predictions would require separate detailed investigations in the form of a completely new set of statistical models and so will have to wait for future analyses of this same data set. However, we can confirm here that bouts became longer due to more V-shaped dives rather than U-shaped dives, probably when fewer prey were present per dive. Indeed, longer runs of U-shaped dives towards the end of the bout appeared to limit the length of the bout, probably because as the gut fills up the marginal gains per prey item changes for further dives, which at some point favours a return to the nest (Stephens & Charnov, 1982).

Longer bouts were thus less likely to involve longer runs of U-shaped dives, and dives later in such longer bouts were less likely to be U-shaped, while longer bouts were more likely to lead to termination of the foraging activity. This suggests that shag foraging activity was terminated once the frequency of success became lower than average, as predicted by the MVT (Charnov, 1976). Dives and bouts at the beginning of a foraging session will have involved fewer stomach contents and thus steeper marginal self-feeding gains per prey item. Likewise, dives and bouts towards the end of a foraging session will have involved more satiated, heavier individuals with fuller stomachs, perhaps experiencing lower marginal gains per prey captured (Charnov, 1976; Houston, 1990; Nonacs, 2001). Thus, when individuals decided to terminate the foraging activity, those last few dives may have been more likely to involve a series of dives without sufficient prey detection, indicating patch depletion, increased relative costs of movement and lower marginal gains per prey captured. Furthermore, more satiated individuals with full stomachs may also have been less willing to take on excessive foraging costs, especially for the purposes of self-feeding, preferring to abort a prey search or even a pursuit with low chances of success in what could have been a U-shaped dive, thereby converting that dive into a V-shaped dive. Having terminated a bout due to low prey capture rates, moving to a new patch and beginning a new dive bout may also be marginally less beneficial for more full individuals than simply returning to the nest and delivering the currently gathered food load to the chicks (Charnov, 1976; Ydenberg & Davies, 2010). All of this means that successive bouts of dives were also likely to have been non-independent from each other. The divisions of dives into bouts were probably based upon the ongoing rate of foraging success in those bouts via the shag’s current (stomach) load size and marginal costs

TABLE 4 Within-individual effects on the dive parameters maximum depth, different dive and surface durations due to dive number within the bout and bout length and any interactions for: (a) "V-shaped" dives ( $n = 16,283$ ) and (b) "U-shaped" dives ( $n = 25,731$ ).

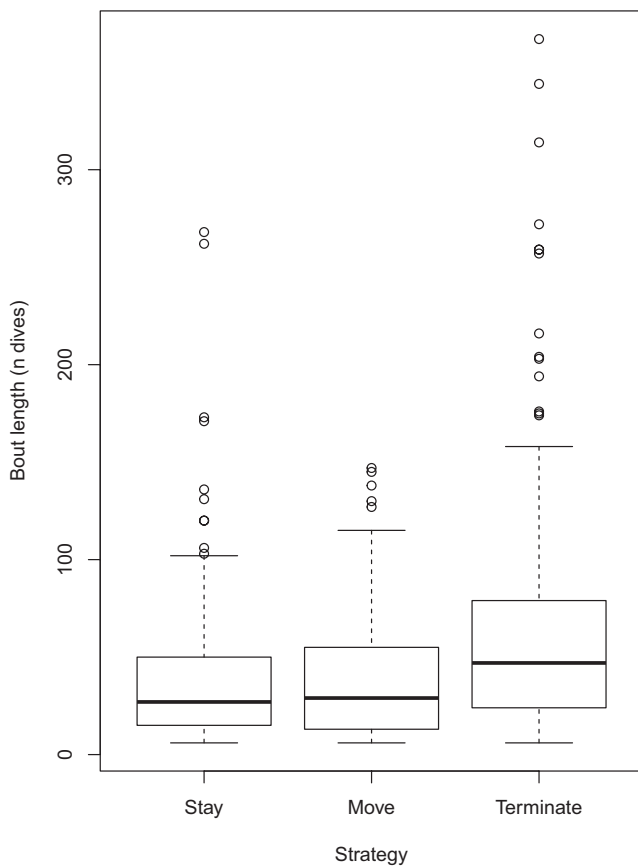
(a) V-Shaped	Max depth (m)	Descent duration (s)	Bottom duration (s)	Ascent duration (s)	Post-dive duration (s)
Intercept	-0.05 (-0.19, 0.10)	0.04 (-0.07, 0.16)		0.12 (0.01, 0.22)	-0.06 (-0.11, -0.03)
Dive number	<b>0.04</b> (0.02, 0.05)	<b>0.02</b> (1.48e-3, 0.04)		1.65e-4 (-0.02, 0.02)	-0.01 (-0.03, 1.78e-3)
Bout length	<b>-0.09</b> (-0.15, -0.04)	<b>-0.06</b> (-0.11, -7.55e-3)		-0.03 (-0.08, 0.02)	<b>-0.17</b> (-0.22, -0.12)
Dive no * bout length	<b>-0.04</b> (-0.06, -0.02)	<b>-0.08</b> (-0.10, -0.05)		<b>-0.06</b> (-0.08, -0.04)	-8.89e-3 (-0.03, 0.01)
IndividualID	0.00	0.00		0.00	0.00
BoutID	0.33	0.22		0.21	0.12
Location	0.07	0.04		0.03	0.00
Year	0.00	0.00		0.00	0.00
Day	0.01	0.00		0.00	0.00
Residual	0.59	0.74		0.76	0.87
R <sup>2</sup> fixed	0.03	0.01		0.02	0.02
R <sup>2</sup> random	0.38	0.25		0.23	0.12
R <sup>2</sup> residual	0.59	0.74		0.75	0.86
(b) U-Shaped	Max depth (m)	Descent duration (s)	Bottom duration (s)	Ascent duration (s)	Post-dive duration (s)
Intercept	1.26 (-0.86, 3.41)	1.37 (-0.18, 2.92)	-0.51 (-2.01, 1.00)	1.42 (0.15, 3.69)	0.63 (-0.97, 2.30)
Dive number	<b>-2.18</b> (-2.73, -1.63)	<b>-1.47</b> (-2.01, -0.89)	<b>-1.98</b> (-2.80, -1.24)	<b>-1.32</b> (-1.82, -0.82)	<b>-2.25</b> (-2.93, -1.60)
Bout length	<b>2.89</b> (0.27, 5.52)	<b>2.34</b> (0.28, 4.49)	<b>3.10</b> (0.84, 5.45)	<b>2.63</b> (0.84, 4.40)	<b>3.76</b> (1.33, 6.06)
Body mass	-0.15 (-0.44, 0.13)	-0.17 (-0.38, 0.03)	0.07 (-0.14, 0.26)	<b>-0.19</b> (-0.35, -0.02)	-0.07 (-0.29, 0.14)
Dive no * bout length	0.34 (-0.61, 1.22)	0.59 (-0.37, 1.48)	0.17 (-1.04, 1.32)	<b>0.87</b> (0.04, 1.69)	0.95 (-0.02, 1.93)
Dive no * mass	<b>0.29</b> (0.22, 0.37)	<b>0.19</b> (0.12, 0.27)	<b>0.26</b> (0.16, 0.36)	<b>0.17</b> (0.11, 0.24)	<b>0.30</b> (0.22, 0.39)
Bout length * mass	<b>-0.41</b> (-0.76, -0.06)	<b>-0.33</b> (-0.61, -0.05)	<b>-0.43</b> (-0.75, -0.13)	<b>-0.37</b> (-0.60, -0.12)	<b>-0.53</b> (-0.83, -0.20)
Dive no * bout length * mass	-0.05 (-0.17, 0.08)	-0.08 (-0.20, 0.05)	-0.03 (-0.18, 0.14)	<b>-0.12</b> (-0.23, -7.93e-3)	-0.13 (-0.26, 7.26e-4)
IndividualID	0.00	0.00	0.00	0.00	0.00
BoutID	0.31	0.20	0.10	0.15	0.15
Location	0.07	0.02	0.00	0.03	0.08
Year	0.00	0.00	0.00	0.00	0.00
Day	0.01	0.01	0.00	0.00	0.00
Residual	0.60	0.78	0.90	0.82	0.77
R <sup>2</sup> fixed	0.03	0.02	0.02	0.02	0.02
R <sup>2</sup> random	0.34	0.21	0.10	0.17	0.21
R <sup>2</sup> residual	0.63	0.77	0.88	0.81	0.77

Note: Asterisk (\*) symbolises interactions. Parameters and explanatory variables were mean centred within individual identity. Mixed-effect models included individual and bout identity, location, year and day as random effects, as proportions of total variation explained. Fixed effects are effect sizes (for non-standardized values)  $\pm 95\%$  CIs, and marginal R<sup>2</sup> values are given for fixed and random effects and the residual variance. Bold numbers indicate significant values, except in intercepts. For model selection, see Table S7. See Table S13 for full data model results and Table S14 for among-individual model results.

**TABLE 5** The relationships between post-bout behaviours of: “Stay” – stayed to forage in the same location; “Move” to a new patch location to forage; or terminated foraging activity “Terminate,” and various dive and bout characteristics: last dive type (with bottom duration “U-shaped” versus no bottom duration V-shaped dives) in bouts; log last run length of V-shaped dives in bout; log last run length U-shaped dives in bouts; and log last bout length in bouts (for Dive type and Log bout length  $n = 931$ ; for Log run length V-shaped  $n = 375$ ; for Log run length U-shaped  $n = 557$ ).

	Last dive Type	Log run length V-shaped	Log run length U-shaped	Log bout length
Intercept (Stay)	0.46 (0.23, 0.69)	0.51 (0.42, 0.60)	0.90 (0.72, 1.06)	3.48 (3.38, 3.57)
Stay vs Move	0.07 (-0.22, 0.34)	2.39 e-2 (-0.11, 0.15)	-0.11 (-0.24, 0.04)	0.05 (-0.04, 0.16)
Stay + Move vs Terminate	-0.05 (-0.16, 0.05)	<b>0.18</b> <b>(4.41 e-4, 0.10)</b>	-0.03 (-0.02, 0.09)	<b>0.12</b> <b>(0.07, 0.16)</b>
IndividualID	0.17	0.03	0.09	0.11
Year	0.00	0.00	0.00	0.00
Location	0.00	0.00	0.03	0.00
Residual	0.83	0.97	0.88	0.89
R <sup>2</sup> fixed	0.00	0.02	-0.01	0.06
R <sup>2</sup> Random	0.05	0.03	0.12	0.11
R <sup>2</sup> Residual	0.95	0.95	0.89	0.83

Note: Mixed-effect models included individualID, location and year as random effects, here given as proportion of total variation explained. Bold indicates significant differences for each level contrasted to the mean of the preceding levels (i.e. Helmert contrasts).



**FIGURE 4** Variation in the raw data showing the length of bouts (number of dives) that end with different post-bout decisions: “Stay” = “Stay in same patch”; “Move” = “Move to new patch”; “Terminate” = “Terminate foraging activity.” Median overall bout length = 37 (bout lengths <5 dives not included).

versus benefits of staying versus quitting the current patch (within or between our “locations”). Thus, the decision of terminating a bout and quitting a foraging patch is likely to have been, at least in part, made some time before the final few dives, and is likely based upon the cumulative trajectory of foraging success during a bout, and even perhaps a series of bouts.

Finally, it should be noted that we detected small but biologically meaningful effects of body mass in many of our analyses. This underlines the importance of including this parameter, not only in studies investigating physiological effects, but also when testing for ecological effects in behavioural foraging strategies. Carlsen et al. (2021) detail the almost complete overlap between the statistical effects of sex and body mass in this same dataset, suggesting that body mass is the biologically meaningful factor here rather than the sex of the individual.

In conclusion, it is clear from our study that consecutive foraging dives are unlikely to be as independent from each other as has been assumed in previous behavioural and physiological studies (Carbone & Houston, 1996; Carlsen et al., 2021; Elliott et al., 2008; Walton et al., 1998; Wilson, 2003). However, this was not due to cumulative physiological effects, thereby supporting the idea that flexible post-dive durations are likely sufficient to allow individuals to offload any CO<sub>2</sub> and recover back to their base-line O<sub>2</sub> level. Thus, shags seem to avoid longer-term O<sub>2</sub> debt and/or lactate build-up and at the same time maintain their body temperatures during bouts of dives. Any correlation between adjacent dives instead seemed to be due to details of shag foraging ecology. The non-independent availability of potential prey across adjacent dives, wider foraging activity decision making based upon rates of cumulative foraging success and thus changes in the marginal value of prey across dive cycles within



bouts and trips are likely explanations. This would suggest that assumptions of dive-to-dive independence in optimality studies are indeed justified, but perhaps only when factors such as dive type and the order of dives within a bout or trip are taken into account as part of any statistical analyses. Although direct measurements of lactate accumulation, thermoregulation and prey availability would be desirable, here we show how using indirect measurements based upon behaviour makes it possible to test via inference hypotheses concerning possible physiological and foraging environment effects on dive strategies. This allows us to convincingly explore effects on dive-cycle parameters not one for individual dives, but in the context of preceding and subsequent dive cycles within a bout, and among bouts in a foraging trip.

#### AUTHOR CONTRIBUTIONS

The study was conceived and developed by Jonathan Wright and Astrid A. Carlsen. Data collection was designed by Svein-Håkon Lorentsen and collected by Svein-Håkon Lorentsen and many field workers, including Astrid A. Carlsen, from 2013 to 2018. Data preparation was performed by Jenny Mattisson and Astrid A. Carlsen, and data analysis was performed by Astrid A. Carlsen and Jonathan Wright. The first draft of the manuscript was written by Astrid A. Carlsen and Jonathan Wright, and all authors contributed with comments and edits to the manuscript, giving their final approval for publishing.

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#### DATA AVAILABILITY STATEMENT

The dataset is published at <https://doi.org/10.5061/dryad.p8cz8w9q1>.

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#### SUPPORTING INFORMATION

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

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