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Prey predictability and preparation versus recovery breathing strategies in European shags *Gulosus aristotelis* (L.) diving in different habitats

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Abstract

A recent study on the diving behaviour of European shags (*Gulosus aristotelis* (L.)) foraging in kelp forests off rocky coasts of Norway suggests surface durations are related only to the duration of the preceding dive, and hence are being used for respiratory recovery. These results contrast with earlier reports concerning shags foraging in highly tidal estuarine waters off the coast of Lundy Island, SW England, where there was a stronger relationship between dive durations and preceding pre-dive surface durations, suggesting the use of preparatory variation in oxygen loading. These two datasets were collected using different methods, and statistically analysed in quite different ways, so the contrasting results here could be due to different methodologies rather than the ecological differences between the two foraging environments. Here, we re-analyse the two datasets using similar statistical methods, and we confirm the contrasting results produced by the two datasets. We, therefore, conclude that shag breathing strategies do differ between these two marine environments, presumably reflecting adaptive facultatively plastic responses to differences in predictability of foraging dive durations. Off the Norwegian coast, unpredictable variation in the depth and availability of pelagic prey in complex environments may require more responsive post-dive respiratory recovery on the surface after each dive. In the more uniform English near-shore environment, however, pre-dive preparatory oxygen loading customised to match predictable dive-to-dive variation in benthic prey depths and foraging durations, may be more time and energy efficient.

KEYWORDS
dive behaviour, dive physiology, dive preparation, dive recovery, foraging behaviour, foraging ecology, marginal value theorem

1 | INTRODUCTION

Air-breathing animals that feed underwater face a resource conflict: food is available only below the surface, and oxygen only above it. The time they can spend searching for food is therefore fully dependent upon the size of their body's oxygen deposit and the metabolic rate during the dives. However, foraging divers often need to repeat dives at a high frequency for extended periods of time in order to meet their energetic needs, and so not only is the energetic cost of a dive important but also the duration of the dive as well as the time needed to replenish the oxygen storage at the surface (Kramer, 1988). In terms of foraging efficiency, time spent on the surface is time during which no prey can be caught; its only purpose is to offload carbon dioxide and replenish oxygen stores. Kramer showed that an optimal diver should not necessarily completely fill its oxygen stores before each dive, and so the factors determining pre- and post-dive surface durations are of large theoretical and empirical interest in relation to optimal dive strategies (see Carbone & Houston, 1996; Houston & Carbone, 1992; Walton et al., 1998). Over a series of dives under given conditions, the more time the diver spends underwater on each dive, the more time it must spend on the surface between dives. In principle, there are two ways in which this relationship can be maintained: by respiratory preparation before a dive, in which the diver remains on the surface before each dive for long enough to absorb enough oxygen to allow for the dive's anticipated duration, or by respiratory recovery, in which the diver remains on the surface after each dive for long enough to restore its oxygen load after the dive's actual duration. However, it is not known whether these two strategies are species specific or induced by different habitats.

This question is brought into sharp focus by the contrast between two studies of the relation between diving and surface times of the European shag (*Gulosus aristotelis* (L.)), a marine cormorant of the eastern North Atlantic and Mediterranean coasts. Carlsen et al. (2021) recently reported an extensive study of shag diving behaviour. Using GPS and time-depth recorders, they observed over 42,000 dives from 39 pairs of male and female shags. Among the questions considered was the relationship between dive duration and the time spent pre-dive versus post-dive on the surface during a bout of dives. They showed a clear link between dive durations and only post-dive duration, suggesting that shags use a strategy of post-dive oxygen recovery in response to the unpredictability of dive depths and durations. These results contrast with earlier findings by Lea et al. (1996), who carried out shore-based observations of 749 foraging dives by European shag, and compared the predictability of dive durations by pre- versus post-dive surface durations, immediately preceding and immediately after each dive. They found that dive duration was better predicted by the pre-dive surface duration than the post-dive surface durations. Accordingly, they concluded that shags in some sense prepare for or anticipate the duration of their next dive and thus take in only an immediately appropriate quantity of oxygen. This was in contrast with their conclusions for three other species of phalacrocoracid, the great cormorant (*Phalacrocorax carbo*

(L.)), the pied shag (*P. varius* (Gmelin)) and the little shag (*Microcarbo melanoleucus* (Viellot)). In the little shag, they found that dive durations were almost exclusively related to post-dive surface durations, while in the great cormorant and the pied shag they were related to both pre-dive and post-dive surface durations. Accordingly, Lea et al. (1996) concluded that their little shags were primarily using recovery breathing, restoring their oxygen levels according to the energetic expenditure and dive duration, whereas great cormorants and pied shags showed a mixture of recovery and preparatory oxygen loading and carbon dioxide dumping, and European shags were essentially preparatory breathers.

To account for the differences between the conclusions of Carlsen et al. (2021) and Lea et al. (1996), both involving European shags, Carlsen et al. (2021) suggested that the statistical analysis carried out by Lea et al. (1996) may have been problematic. Because Lea et al. (1996) used shore-based observations, they could not identify individual birds; they also used the diving bout identifier as a fixed factor, whereas it would be better considered as a random factor in a mixed-effect model. Carlsen et al. (2021) considered that this might have biased the analysis towards producing apparent evidence for preparatory pre-dive oxygen loading, as they were able to show a possibly similar artefact as part of among-individual (as opposed to the more appropriate strictly within-individual) comparisons in their own data. They, therefore, suggested that conclusions reached by Lea et al. and other authors using similar analysis methods such as Butler and Woakes (1979), Sato et al. (2002), Stephenson et al. (1986), Wilson (2003) and Elliott et al. (2008) might be called into question. However, the suggestion that the inability to identify individuals might have biased the results of Lea et al. (1996) towards an appearance of preparatory breathing seems unlikely for two reasons. Firstly, although Lea et al. could not separate data for analysis according to the individual bird, they did separate their data according to diving bouts, and ensured that each bout only involved a single individual. All comparisons were made within bouts, and so were within individual, although the number of independent individuals in the analysis was likely to be substantially lower than the number of bouts. Secondly, using the same observational and statistical analysis methods for species other than the European shag, Lea et al. were able to find evidence of some responsive oxygen recovery in post-dive surface durations, and in the case of the little shag, they found no evidence of preparatory oxygen loading using variation in pre-dive surface durations.

If the contrasting statistical methodologies used are not the explanation, it remains possible that the contrasting conclusions reached by Carlsen et al. (2021) and Lea et al. (1996) reflect real biological differences in foraging dive behaviour between the two different study populations of European shags. Indeed, Carlsen et al. (2021) provided an interesting ecological explanation as to why they saw no evidence for the kind of preparatory dive strategy found by Lea et al. (1996), especially in a number of other studies on species like diving ducks (e.g. Butler & Woakes, 1979; Carbone & Houston, 1996; Stephenson et al., 1986). They suggested that the greater variation in hunting (as opposed to

non-hunting sampling) dive durations in their data may reflect the fact that their shags were searching for and hunting pelagic fish in a highly stochastic foraging environment. In kelp forests off the rocky coast of Norway, shags may not be able to accurately anticipate their dive durations in a way that would be much easier for benthic feeders foraging on more predictable prey locations in an evenly sandy-bottomed bay, such as off the shore of Lundy Island. This type of greater dive-to-dive variation in hunting and pelagic prey pursuit dive durations is also seen in Weddell seals (Kooyman et al., 1980). So, although the diving physiologies of many diving birds may be similar, their foraging niches can be distinctively different, requiring contrasting dive cycle strategies, and such behavioural differences are likely to also be found in other groups of diving animals, such as mammals. For species feeding on more predictably distributed benthic prey, pre-dive preparation may be the more efficient dive cycle strategy, as the individual can anticipate to a large extent how long a foraging dive should last and exactly how much oxygen to load, at least after the first dive or so at a certain location (Stephens et al., 2008). However, diving animals foraging on solitary or shoaling pelagic prey, especially in complex marine environments with perhaps decreased visibility, must have a harder time adjusting pre-dive durations to match dive-to-dive variation in the duration and energy expenditure of hunting dives. In such unpredictable foraging conditions, a diving animal should instead use post-dive surface durations which provide much more flexibility in terms of amount of recovery effort needed from the previous dive. Recovery thus includes the basic preparation needed to start any new dive, in as much as it returns the individual to the normal average preparatory state of oxygen stores ready for the next expected average dive duration, as proposed by Wilson and Quintana (2004). This explanation predicts the existence of facultatively plastic dive strategies by foraging divers, like shags, in their relative uses of "preparatory" versus "recovery" dive cycle tactics, in accordance with the predictability of the foraging environment and the depth of the prey in the water. Therefore, ecologically different marine foraging environments could explain Lea et al.'s (1996) contrasting findings in this regard across different species of shags and cormorants, and specifically the differences in European shag diving strategies as compared to Carlsen et al. (2021).

To distinguish between these methodological confounds versus the more interesting biological explanations for the differences between these two studies on European shag diving behaviour, we have analysed the datasets from both studies using the same advanced statistical methods. Because they were using time–depth recorders, Carlsen et al. (2021) were able to collect much more detailed data than Lea et al. (1996), and it is not possible to reproduce their analyses in full using the Lea et al. dataset. However, the measures taken by Lea et al. are all included within the Carlsen et al. dataset, so it is possible to carry out a similar kind of analysis to that used by Lea et al. using the Carlsen et al. dataset, and that is what we have done here. In consequence, the quantitative results from analyses of the Carlsen et al. dataset here differ somewhat to their

findings in the original paper. However, we have also been able to carry out a much simplified version of the Carlsen et al. analysis on both datasets, and those results are reported here for comparison.

2 | METHODS

Procedures for the collection of the two datasets have been fully described in the original publications, Lea et al. (1996) and Carlsen et al. (2021), and so here we provide only a brief description.

2.1 | Lundy dataset

Lea et al. (1996) analysed data from 749 European shag dives from 85 bouts, collected during the early spring of 1990, 1991 and 1992 from the island of Lundy in the Bristol Channel, SW England; almost all of them were collected from observation points around the Landing Bay of the island (51°10′ N, 4°39′ W). The Landing Bay forms a broad ENE-facing arc, with relatively sheltered water given the prevailing south-westerly winds at Lundy. Divers' reports, and observations at low spring tides and times of clear water, show that the sea bottom is mainly composed of sand, pebble and rock. Most observations were made of shags within 500 m of the shore, meaning that water depths from chart datum ranged up to 10 m; however, the tidal range at Lundy is extreme and could add up to 5 m to that depth. Shags show dietary flexibility, according to location and season. Studies around Great Britain have generally found that shags' dominant prey is sandeels (family Ammodytidae), especially during the breeding season, when our observations were made (Howells et al., 2018); and the Bristol Channel is an important spawning ground for sandeels (Ellis et al., 2012). It is likely, therefore, that the shags observed from Lundy were feeding predominantly on sandeels.

For the present analyses, we added to the dataset further observations made in the same location and in an identical way during the early spring of 1994, 1999 and all years from 2005 to 2009; these observations were collected in the course of other research about shag behaviour and have not previously been published. A total of 3068 dives, from 292 bouts, were available for analysis; in 2632 of these cases, from 250 bouts, the surface durations both before and after the dive had been recorded. The full dataset is referred to below as the Lundy dataset, to distinguish it from the dataset originally analysed by Lea et al. (1996). It has been deposited at https://osf.io/d47n2.

2.2 | Sklinna dataset

Carlsen et al. (2021) analysed data from 42,014 dives, collected during 1289 bouts in the period 2013–2018 from shags nesting on the Sklinna archipelago (65°12′ N 10°59′ E), about 20 nmi off the coast of Vikna, Central Norway. The shags foraged mainly in kelp forests in the area around the breeding colony, with rapidly varying

depths (i.e. from 300 m depth to surfacing archipelagos within short distances), strong winds and considerable waves. The main prey in the period was likely to be juvenile pelagic fish species, mainly 0–1 group cod species such as saithe (*Pollachius virens* (L.)) and poor cod (*Trisopterus minutus* (L.)) (Hillersøy & Lorentsen, 2012). Their dataset is referred to below as the Sklinna dataset. It is deposited at https://doi.org/10.5061/dryad.p8cz8w9q1. Further analyses of trends in these data have recently been reported by Carlsen et al. (2023).

2.3 | STRANGEness considerations

Webster and Rutz (2020) argue that researchers should consider how representative the study animals they have sampled are in respect of Social background, Trappability, Rearing history, Acclimation, Natural changes in responsiveness, Genetic makeup, and Experience (the STRANGE framework) Full details of the provenance and selection of animals for data collection are given in the two papers that were first reported on these datasets, Carlsen et al. (2021) and Lea et al. (1996). In the case of the Lundy dataset, observations were made from the shore so birds that habitually foraged far from land would be excluded from the sample. All birds observed were apparently adults based on their plumage, but age could not be determined exactly, and sex could not be observed at all. In the case of the Sklinna dataset, all birds used were nesting adults. Those nesting more accessibly and defending their nests more actively were selected for study as they could be captured for attaching telemetry devices more easily, reducing the disturbance of the nesting colony. Once birds had been selected for observation, none were discarded in either study, but dives were discarded from the datasets for two reasons: dives that occurred in very short bouts, of only one or two dives, could not be included in the analysis; and dive or surface times that were much longer than the average were excluded in some analyses (details are given in the next section).

2.4 | Data analysis

All analyses were carried out using R, version 3.6.1 (R Core Team, 2014). Two major types of analysis were carried out. Both used the R function for linear mixed-model analysis lmer, with measurements of dive and surface times nested within dive bouts, which were treated as a random effect. In Carlsen et al.'s (2021) analyses, bout identifiers were further nested within individual shags, also treated as a random effect. This could not be done for the Lundy dataset, so to make the analyses comparable, it was not done in the present analyses of the Sklinna dataset. However, all the Sklinna analyses reported here were repeated with the additional level of nesting, and this procedure confirmed what would be expected that it made only tiny differences to the relationships involving the within-bout measurements (i.e. the dive and surface durations). The basic unit for all the analysis was a dive duration together with its preceding and succeeding surface durations: this group of three

durations is referred to below as an "extended dive cycle." Results for all analyses of the Sklinna dataset are reported to one further degree of precision than results from the Lundy dataset because of the much larger sample size available.

The first major type of analysis used dive duration as dependent variable, and the pre-dive and post-dive surface durations as independent variables. This replicates the analysis used by Lea et al. (1996) but used the dive bout identifier as a random effect, rather than as a fixed factor in an analysis of covariance. For the Sklinna dataset, this analysis was applied to the four major subsets of the dataset, male and female birds making U-shaped (active "hunting") and V-shaped ("sampling," prey searching) dives – see Carlsen et al. (2021) for more information.

The second major type of analysis used path analyses, examining the structure of the dependence of dive duration on pre-dive surface duration, and post-dive surface duration on dive duration and pre-dive surface duration. These analyses were based on the procedure used by Carlsen et al. (2021) but were limited to using only the variables that were available in the Lea et al. (1996) dataset. The first path considered had dive duration as the dependent variable and pre-dive surface duration as the independent variable; the second path took post-dive surface duration as the dependent variable, with pre-dive surface duration and dive duration as independent variables.

Several different versions of each analysis were run, using different restrictions or transformations of the datasets, in order to investigate the effects of differences in the procedures used in the original papers of Lea et al. (1996) and Carlsen et al. (2021). In particular, Lea et al. removed from their dataset any extended dive cycles that included observations that were more than 3 standard deviations from the grand mean of that type of data (surface duration or dive duration), whereas Carlsen et al. did not. On the other hand, Carlsen et al. log-transformed both surface and underwater times to provide normally distributed residuals and to account for the biologically expected curvilinear effects, but Lea et al. did not. For the present study, both datasets were analysed both with and without each of these modifications. In addition, we considered the dive cycles in which dive or surface durations had been discarded as outliers to examine whether these data might show different effects from the more typical observations. In principle, this analysis could have been carried out on both datasets, but in the Lundy dataset the number of cases excluded as outliers was too small for the analysis to be reliable, so only the Sklinna dataset was used.

Finally, we investigated whether differences in observation technique could have caused the difference in results between the two studies. The Lundy data were collected using visual observation, whereas the Sklinna data were collected using biologging devices. Both techniques can distort the results. With visual observation, the moment of submerging could be identified precisely, whereas with biologging it was inferred from a recorded depth of 1 metre; given the typical speeds of descent, this would transfer about 1 second from dive duration to the preceding surface duration. On the other hand, visual observers could not always be sure of noticing

immediately when a bird re-surfaced, so some time belonging to the post-dive surface duration might be transferred to the dive duration. Lea et al. (1996) used multiple observers to minimise this problem, but could not be sure of eliminating it entirely, and it seems more likely to make a material difference than any delay in counting the start of a dive under biologging. To test whether observers' delay in noticing re-surfacing could have produced the difference in results found in the two datasets, we simulated observer error in the Sklinna dataset by adding random intervals of up to 12 s to each dive time and subtracting it from the subsequent surface time (and therefore from the preceding surface time in the next dive cycle). These analyses were run using the Lea et al. procedure with outliers excluded since the main analyses had shown that excluding them provided more reliable regression estimates. Table 1 lists the selections of data analysed and shows the numbers of complete extended dive cycles available for each, and also the mean and interquartile ranges of the dive and surface durations within them. All R scripts, and the detailed results from them, are included in the deposit at https://osf.io/d47n2.

3 | RESULTS

3.1 | Analysis using analysis of covariance (as in Lea et al., 1996)

We applied Lea et al.'s (1996) procedure to the two datasets, with and without exclusion of outliers and with and without log transformation. In the case of the Sklinna dataset, we applied these procedures to the four different categories of dive that Carlsen et al. (2021) recorded (U-shaped and V-shaped for male and female shags). We also applied them to the subset of dive cycles that we excluded from the main analyses of the Sklinna dataset as outliers.

In the Lundy dataset, the regression coefficients of dive duration on pre-dive surface durations were positive (Table 2), even though the analysis took into account the association between pre- and post-dive surface durations. However, the regression coefficients of dive duration on post-dive surface duration did not differ significantly from zero, except in the analyses where the data were log transformed, and even in that analysis these coefficients were smaller than those for the pre-dive surface time. These results held regardless of whether outliers were excluded, and regardless of whether log transformations were applied. Therefore, in the Lundy dataset, there was clear evidence of a "preparatory" effect, and at most weak evidence of a "recovery" effect.

On the other hand, in the Sklinna dataset, the regression coefficients of dive duration on pre-dive surface duration and post-dive duration (also shown in Table 2) were both consistently positive, with the coefficients on post-dive duration being markedly larger. Therefore, this dataset showed evidence of both "preparatory" and "recovery" effects, with the recovery effect being the stronger of the two. These results held regardless of whether outliers were excluded, and regardless of whether log transformations were applied.

In both datasets, removing outliers using the procedure of Lea et al. (1996) resulted in larger regression coefficients, whether or not the data were log transformed. Similar trends were found in all four major subsets of the Sklinna dataset, although the regression coefficients for V-shaped dives in females were substantially lower than for males or for the overall analysis. On the other hand, the trends shown in the remainder of the dataset are not found within the dive cycles rejected as outliers, suggesting that the removal of these unusual values was justified.

3.2 | Path analyses (reduced form of the analysis of Carlsen et al., 2021)

Figure 1 shows the structure of the path analysis, and also includes quantitative results for the version of it most similar to the analysis in Carlsen et al. (2021), for comparison with the figures in that study. In Path 1, with dive duration as the dependent variable and pre-dive surface duration as the independent variable, both datasets led to positive regression coefficients, as shown in Table 3. However, because no other variable was included in the corresponding regression, this association could be due to the general covariation between durations within dive cycles expected within a bout of dives. In Path 2, where post-dive surface duration was the dependent variable, with pre-dive surface duration and dive duration as independent variables, both datasets showed positive coefficients of post-dive surface durations on pre-dive surface duration, independent of the association between dive time and post-dive surface durations. The datasets differed, however, in the size of the regression coefficients of post-dive surface duration on dive duration, the indicator for a "recovery" effect. The coefficients in the Sklinna dataset were substantially larger than those for the Lundy dataset. All these results held true regardless of whether outliers were excluded, and regardless of whether log transformations were applied. As in the analyses of covariance, excluding extended dive cycles containing outliers generally resulted in greater effect sizes. However, this tendency was not completely uniform, with a few coefficients being effectively unchanged.

3.3 | Simulating the effect of observer error

To test for the possibility that delay in noticing re-emergence of the shags had distorted the results from the Lundy dataset, we simulated such an effect in the Sklinna dataset, using the analysis procedure of Lea et al. (1996). In these analyses, we transferred a random 0–1, 0–6 or 0–12 s from each dive duration to the succeeding surface duration. The results are shown in Table 4: the transfer did inflate the evidence for a preparatory effect (coefficient of dive duration on preceding surface duration) and reduce the evidence for a recovery effect (coefficient of dive duration on succeeding surface duration), but only by a relatively small amount. As would be expected, the larger the simulated observer error, the greater the shift towards a

TABLE 1 Datasets used for analysis.

Description	Number of extended dive cycles included	Number of diving bouts included	Median and interquartile range of	
			Dive duration (s)	Surface duration (s)
Lundy data full dataset	2632	250	41.9 (34.0–51.2)	15.0 (11.0–19.9)
Lundy data excluding outliers	2529	243	41.2 (34.0–50.0)	14.6 (11.0–19.0)
Sklinna data full dataset	42,014	1030	30.0 (20.0–42.0)	18.0 (12.0–30.0)
Sklinna data excluding outliers	40,095	1005	30.0 (20.0–42.0)	18.0 (10.0–28.0)
Sklinna data excluding outliers, males, V-shaped dives	5208	440	30.0 (18.0–40.0)	18.0 (10.0–28.0)
Sklinna data excluding outliers, females, V-shaped dives	10,297	504	18.0 (8.0–28.0)	18.0 (10.0–28.0)
Sklinna data excluding outliers, males, U-shaped dives	10,613	450	42.0 (32.0–50.0)	18.0 (10.0–28.0)
Sklinna data excluding outliers, females, U-shaped dives	13,977	505	30.0 (22.0–40.0)	18.0 (10.0–28.0)
Lundy full dataset, log transformed	2632	250	3.74 (3.53–3.94) log seconds	2.71 (2.40, 2.99) log seconds
Lundy data excluding outliers, log transformed	2529	243	3.72 (3.53–3.91) log seconds	2.63 (2.40, 2.94) log seconds
Sklinna full dataset, log transformed	42,014	1030	3.40 (3.00, 3.74) log seconds	2.89 (2.49, 3.40) log seconds
Sklinna data excluding outliers, log transformed	40,095	1005	3.40 (3.00, 3.74) log seconds	2.89 (2.30, 3.33) log seconds
Sklinna dataset, surface–dive–surface cycles involving at least one outlier	1918	511	44.0 (26.0–70.0)	105.0 (36.0–178.0)
Sklinna data excluding outliers, with simulated observer error of up to 1, 6 and 12s	39,198	987	30.5 (20.1, 42.1) 32.9 (22.2, 44.2) 36.0 (24.9, 47.4)	17.2 (10.0, 27.5) 14.4 (7.9, 25.2) 11.7 (4.8, 22.6)

Note: Outliers were defined as durations more than 3 standard deviations from the relevant grand mean. Where outliers were excluded, the presence of an outlier in any of the durations in an extended dive cycle meant that the entire cycle was excluded from the analysis.

TABLE 2 Results of applying the analytic approach of Lea et al. (1996) to the data collected at Lundy and Sklinna, treating bout effects as random, with duration measurements nested under bout only.

Analysis details	Lundy dataset		Sklinna dataset	
	Coefficient of preceding surface time	Coefficient of succeeding surface time	Coefficient of preceding surface time	Coefficient of succeeding surface time
Entire dataset, untransformed (i.e. no exclusion of outliers, no log transformation)	**0.16 (0.11, 0.20)**	0.01 (−0.03, 0.05)	**0.041 (0.037, 0.044)**	**0.078 (0.074, 0.082)**
Outliers excluded, no log transformation	**0.21 (0.15, 0.27)**	0.06 (−0.00, 0.12)	**0.108 (0.101, 0.114)**	**0.177 (0.170, 0.183)**
Entire dataset, log transformed	**0.11 (0.09, 0.14)**	**0.03 (0.003, 0.06)**	**0.113 (0.105, 0.121)**	**0.188 (0.180, 0.196)**
Outliers excluded, data log transformed	**0.11 (0.08, 0.14)**	**0.06 (0.03, 0.09)**	**0.141 (0.132, 0.150)**	**0.225 (0.166, 0.180)**
V-shaped (exploratory) dives, males, outliers excluded			**0.122 (0.105, 0.140)**	**0.191 (0.173, 0.208)**
V-shaped dives, females, outliers excluded			**0.053 (0.041, 0.064)**	**0.060 (0.049, 0.072)**
U-shaped (foraging) dives, males, outliers excluded			**0.118 (0.106, 0.129)**	**0.227 (0.215, 0.239)**
U-shaped (exploratory) dives, females, outliers excluded			**0.145 (0.133, 0.157)**	**0.203 (0.191, 0.215)**
Data initially discarded as outliers			**−0.032 (−0.044, −0.021)**	−0.006 (−0.013, 0.010)

Note: Results shown are regression coefficients, with their 95% confidence intervals in parentheses. Regression coefficients with confidence intervals not overlapping zero are shown in bold. Outliers were defined as described in Table 1.
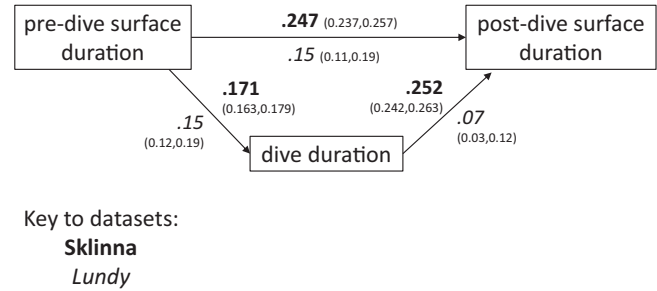

Key to datasets:
Sklinna
Lundy

FIGURE 1 Results of applying a simplified path analysis based on that used by Carlsen et al. (2021) to the extended dive cycle in both the Lundy and Sklinna datasets. As in Carlsen et al.'s analysis, data were log transformed, and no exclusion of outliers was used. Estimates shown are standardised regression coefficients (β values) from the structural equations in Table 3.

preparatory effect, but even at unrealistically high levels, it did not reverse the tendency for the recovery effect to be greater than the preparatory effect. Thus, it seems unlikely that the difference in results between the two datasets is due to the differences in observation techniques.

4 | DISCUSSION

The results from all versions of the statistical analyses confirm the different nature of the breathing patterns in the two European shag datasets. The Lundy data predominantly show "preparatory" use of flexible oxygen loading in pre-dive surface durations, while the Sklinna data predominantly show variation in post-dive surface durations consistent with a "recovery" strategy. Furthermore, the difference in these results remained even when simulating in the Sklinna dataset the types and scale of observer errors that may have occurred in the Lundy dataset. This establishes that the difference in the results reported by Lea et al. (1996) and Carlsen et al. (2021) did not arise from their different field methodologies or statistical approaches. It, therefore, seems safe to conclude that the contrasting results reflect real biological differences in the behaviour and/ or ecology of the shags in the two study populations. We, therefore, conclude that breathing strategy is not, as Lea et al. (1996) suggested, a species characteristic, but rather that it can be adapted flexibly to different conditions. We cannot tell from our data whether the flexibility results from long-term individual differences, or from relatively short-term behavioural flexibility within individuals. However, the results of Watanuki et al. (2008), using cameras attached to foraging shags, suggest that individuals switch flexibly between rocky and sandy undersea areas, so individual flexibility seems a likely explanation.

When the two datasets are analysed in the same way, the primary difference between them that emerges is the need for "recovery" breathing. The regression coefficients for the association between the preceding surface time and the underwater time are roughly similar for the two studies. However, the recovery effect is

TABLE 3 Path analysis of the effects of pre-dive surface duration on post-dive surface duration and dive duration.

	Lundy dataset			Sklinna dataset		
	Path 1	Path 2		Path 1	Path 2	
Analysis details	Pre-dive surface duration on dive duration	Pre-dive surface duration on post-dive surface duration	Dive duration on post-dive surface duration	Pre-dive surface duration on dive duration	Pre-dive surface duration on post-dive surface duration	Dive duration on post-dive surface duration
Entire dataset, untransformed (i.e. no exclusion of outliers, no log transformation)	**0.11** (0.08, 0.14)	**0.17** (0.12, 0.21)	**0.08** (0.03, 0.13)	**0.096** (0.089, 0.104)	**0.126** (0.116, 0.135)	**0.277** (0.265, 0.288)
Outliers excluded, no log transformation.	**0.11** (0.08, 0.15)	**0.22** (0.18, 0.27)	**0.12** (0.07, 0.16)	**0.166** (0.158, 0.174)	**0.184** (0.174, 0.194)	**0.323** (0.311, 0.334)
Entire dataset, log transformed	**0.15** (0.12, 0.19)	**0.15** (0.11, 0.19)	**0.07** (0.03, 0.12)	**0.171** (0.163, 0.179)	**0.247** (0.237, 0.257)	**0.252** (0.242, 0.263)
Outliers excluded, data log transformed	**0.15** (0.11, 0.18)	**0.14** (0.10, 0.19)	**0.13** (0.09, 0.18)	**0.196** (0.188, 0.205)	**0.245** (0.235, 0.255)	**0.273** (0.263, 0.284)

Note: Entries are standardised regression coefficients (β values), with 95% confidence intervals in parentheses. Values with confidence intervals not overlapping zero are shown in bold. Outliers were defined as described in Table 1.

TABLE 4 Results of simulating, within the Sklinna dataset, observer errors of the kind that might occur in the Lundy dataset, using the analysis techniques of Lea et al. (1996).

Time transferred (s)	Coefficient of dive duration on preceding surface duration	Coefficient of dive duration on succeeding surface duration
0	**0.108** (0.101, 0.114)	**0.177** (0.170, 0.183)
0–1	**0.106** (0.099, 0.113)	**0.178** (0.171, 0.184)
0–6	**0.107** (0.100, 0.114)	**0.164** (0.157, 0.170)
0–12	**0.114** (0.107, 0.121)	**0.123** (0.116, 0.130)

Note: A random amount of time was transferred from each surface duration to the preceding dive duration, to simulate the effects of visual observers failing to notice immediately when a shag re-surfaced after a dive. Results shown are regression coefficients, with their 95% confidence intervals in parentheses. Regression coefficients with confidence intervals not overlapping zero are shown in bold. Outliers as described in Table 1 were removed before analysis.

mostly absent in the Lundy dataset and consistently the strongest effect shown in the Sklinna dataset. It seems that in both environments, staying on the surface longer enables the birds to stay underwater longer on the next dive, but only in the Sklinna dataset does a longer time underwater require a longer recovery time immediately afterwards. What differences in the foraging environments might produce this behavioural difference? We argue that two are likely to have been relevant: the energetic cost of foraging and the predictability of the prey distribution. We examine each of these in turn.

The data strongly suggest that foraging was more energetically expensive for the shags at Sklinna than at Lundy. The medians and interquartile ranges of the surface and underwater times in the two samples show that the Lundy birds were spending less time on the surface, but longer underwater, than the Sklinna sample (Lundy vs. Sklinna medians of 15.0 vs. 18.0 s on the surface, and 41.9 s vs. 30.0 s underwater: see Table 1). This comparison implies a greater oxygen need per unit time, and hence a greater average energy expenditure, during dives in Sklinna. Greater dive-specific costs would mean

that a marginal increase in dive time would lead to a requirement for a corresponding increase in the next recovery time (Chimienti et al., 2017; Grémillet & Wilson, 1999).

Why would the birds at Sklinna have incurred higher dive-specific costs than their conspecifics at Lundy? Existing literature on diving energetics, especially in phalacrocoracids, suggests a number of factors that may have been responsible. There are two that we believe we can dismiss, namely sea temperature and the use of time–depth recorders. Colder temperatures make diving more costly (e.g. Enstipp et al., 2006; Grémillet & Wilson, 1999), and Sklinna is substantially more northerly than Lundy and has colder water overall. However, the Sklinna data were collected in June and July, and at that time, nearby surface sea temperatures range between 8 and 16°C (figures for Trondheim from https://www.seatemperature.org/europe/norway/trondheim-june.htm); the Lundy data were collected in April, when surface sea temperatures at the nearest measurement station range from 8.0 to 10.9°C (https://www.cefas.co.uk/data-and-publications/sea-temperature-and-salinity-trends/results/stati

on-27-ilfracome/). A second factor that might have been relevant is the fact that the Sklinna shags were fitted with time–depth recorders, whereas the Lundy shags were not; although the recorders weighed less than 2% of the birds' body weight, Vandenabeele et al. (2015) have shown that such devices can have a disproportionate effect on the energy required for underwater foraging. However, Vandenabeele et al. calculate an increase in energy costs of 7% for a device weighing 3% of the forager's body mass, so any effect on the Sklinna shags should have been less than this and seems unlikely to cause the birds to adopt an entirely different breathing strategy.

Two other factors probably were relevant. One is the depth of diving: in the Sklinna dataset, the median value for the maximum dive depth of U-shaped active hunting dives was 7.47 m, whereas the Lundy landing bay has water depths and thus maximum prey depths that quickly reach 10 m below mean low tide level (with tidal swings of up to 7 m to be taken into account additionally). Shallow dives come with higher buoyancy-related costs than deeper dives, and buoyancy is by far the highest dive-specific cost (Ribak et al., 2004). Secondly, at Sklinna, the shags had to engage in actively searching for and chasing around pelagic prey, mainly young gadoids (Hillersøy & Lorentsen, 2012), within kelp forests and with strong tidal currents, whereas the shags' dominant prey around Lundy are the relatively sessile, benthic sandeels, and the sea floor in the Lundy landing bay has substantial areas of mud, sand and pebble (see Methods for site descriptions). In tank experiments with double-crested cormorants (*Nannopterum auritum* (Lesson)), Halsey et al. (2007) have shown that the foraging phase of a dive was more energetically expensive when the birds hunted pelagic, motile prey rather than sessile benthic prey.

As well as making foraging at Sklinna more energetically expensive, this difference in the undersea environment will also have made it less predictable. The sea bottom where the Sklinna shags forage is steeply sloping (see https://kart.kystverket.no/) and covered in dense kelp forest (Christensen-Dalsgaard et al., 2017), with pelagic fish prey being available at many possible depths and locations. In contrast, the sea bottom around Lundy slopes relatively gradually (see https://fishing-app.gpsnauticalcharts.com), and the shags were fishing predominantly for benthic prey. The Lundy shags would therefore be less prone to unplanned dive-to-dive variation in foraging depths, dive durations and energetic swimming expenditures compared to the Sklinna shags. This would have allowed "preparatory" planning of customised levels of pre-dive oxygen loading to match the predictable expected demands of the next dive by the shags around Lundy, as Cook et al. (2010) have suggested occurs in Kerguelen shags (*Leucocarbo verrucosus* (Cabanis)). In comparison, the Sklinna shags did not have the luxury of this strategy and had to rely upon "recovery" post-dive oxygen replenishment to match the widely varying dive depths, durations and energy costs between the dives within a bout.

A second source of unpredictability for the Sklinna shags is the fact that their prey included some relatively large fish (Hillersøy & Lorentsen, 2012), and the birds would probably surface as soon as they had caught one. Shags feeding on sandeels, on the other hand, may take several fish on a single dive (Wanless et al., 1993, estimate

a mean of 7.2), so their behaviour has something in common with grazing. Watanuki et al. (2008) have reported a "recovery" effect in shags foraging for butterfish (*Pholis gunnellus*) under conditions where they frequently return to the surface with a fish in their bill, although they do not report data relevant to any "preparatory" effect. It is notable that the little shags which Lea et al. (1996) reported to show only recovery breathing frequently surfaced with fish of quite substantial size (flounders, probably *Rhombosolea* sp.) in their bills.

Consistent with this analysis, the Lundy shags were close to the diving efficiency of 2.8 to 3.0 for the species that were reported by Dewar (1924, table 12), whereas the Sklinna shags showed a lower efficiency: based on the median dive and surface times shown in Table 1, efficiency was 2.79 in the Lundy dataset and 1.67 in the Sklinna dataset. The Lundy shags' behaviour was therefore closer to that of an optimal diver, which according to Kramer (1988) should exhaust its oxygen stores to the same level on each dive at a given depth, and thus would not be expected to show any recovery effect. A bird that resurfaces as soon as it has caught a fish is unlikely to behave in such a way.

In terms of the STRANGEness of our study samples (Webster & Rutz, 2020), our samples cannot be taken to be representative of all the shags at either the Sklinna or the Lundy breeding colony. At Sklinna, they represent only those currently breeding, and within that group, those that were easier to capture for attaching telemetry devices. There is no obvious reason why the latter restriction would interact with breathing patterns, although it might select for bolder individuals. At Lundy, our sample includes only shags feeding inshore, and birds were sometimes seen flying further from land. In light of the analyses reported here, it is certainly possible that birds feeding further from the island would show different breathing patterns – but that would only support our current conclusions, not invalidate them.

So far as we are aware, the present paper is the first report of within-species variation in the breathing strategies of a diving bird. However, it joins several papers that have shown that other aspects of diving are subject to within-species, probably facultative, variation. For example, maximum depth and preferred time of day for foraging have been shown to vary between the sexes in Crozet shags (*Leucocarbo melanogenis* Blyth: Cook et al., 2007), and between individuals in both European shags and blue-eyed shags (*L. atriceps* (King)); in both these species, dive depth also increased with light availability (Wanless et al., 1999). Chimienti et al. (2017) showed that common guillemots (*Uria aalge* (Pontoppidan)) switched between pursuing pelagic and benthic prey according to their relative availability. An opportunistic diving species like the European shag, which takes a wide array of prey types (Hillersøy & Lorentsen, 2012), would be expected to switch easily between foraging strategies (Grémillet & Wilson, 1999) depending upon the focal prey species of interest in any particular foraging site.

In conclusion, the differences between European shags' foraging dive strategies reported by Lea et al. (1996) versus Carlsen et al. (2021) appear to be real, rather than an artefact of the

differences in methods and statistical modelling between the two studies. They are therefore likely to be due to the ecological differences between the foraging environments in Lundy versus Sklinna. The strategic use of more efficient "preparatory" pre-dive oxygen loading to match expected variation in the costs per foraging dive at Lundy seems appropriate given the predictability of (benthic) prey depths and availabilities within a tidal bay. In contrast, the less predictable depths of pelagic prey, and the more variable and cluttered rocky kelp forest foraging environment at Sklinna probably require greater and more variable energy expenditures per dive, which in turn requires the more responsive post-dive "recovery" of oxygen stores. We would expect similar differences in breathing strategy within other species that dive into varying underwater environments. Further work is now needed to test these hypothesised relations between foraging ecologies and European shag breathing strategies at these two sites, and in general, to link avian diving physiology to different prey acquisition behaviours.

AUTHOR CONTRIBUTIONS

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DATA AVAILABILITY STATEMENT

All data, analysis scripts and primary output are available in public depositories https://osf.io/d47n2 and https://doi.org/10.5061/dryad.p8cz8w9q1.

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