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# Foraging behaviour of the European shag during early chick-rearing period; do they follow the marginal value theorem?

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# Summary

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**1.** Optimal allocation of food is essential during the breeding season, when animals have to provide food for themselves and their chicks. As central place foragers, seabirds forage away from the nest and have to balance their travelling and foraging times and their food intake so that their energy gain is optimized in order to sustain for themselves and their offspring. The marginal value theorem (MVT) predicts an optimal residence time in a foraging patch in response to the rate of energy intake and travelling time to the patch.

**2.** The breeding performance of seabirds is closely related to the availability of food and their individual foraging performance. Thus, it is important to understand their foraging strategies in order to manage populations successfully.

**3.** In this study, GPS loggers (Global Positioning System) and TDR's (Time Depth Recorders) were used simultaneously to collect data on foraging behaviour of European shags *Phalacrocorax aristotelis* during the early chick rearing period at Sklinna, central Norway. Individual variation in foraging behaviour was investigated in accordance with the predictions of the MVT.

**4.** The results showed that shags foraged in a patchy habitat and that the distance to the colony was an important predictor of the time spent in the foraging patch, time spent diving and time spent resting. However, assuming that dive time is positively correlated with prey acquisition, the shags did not experience a diminishing return while foraging, which is an important assumption of the MVT.

**5.** The principles expressed in the MVT may govern allocation of foraging behaviour of European shags. Accordingly, factors that influence optimal foraging behaviour may have consequences for the total energy budget and their chick production, and ultimately their lifetime reproductive success.

**Key-words:** European shag *Phalacrocorax aristotelis*, marginal value theorem, optimal foraging, sexual dimorphism, time-budget



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# Introduction

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Many seabirds aggregate in breeding colonies to raise their chicks, but their food resources are often not found in the vicinity of the colony (Coulson 2002; Grémillet *et al.* 2004a; Burke & Montevecchi 2009). Accordingly, as central place foragers, they feed away from their breeding colonies and, thus, have to carry the food from their foraging areas to their nests to provide food for their chicks (Orians & Pearson 1979). Therefore, in order to maximize their foraging efficiency during a trip, seabirds have to balance their travelling and foraging times and their food intake so that their energy gain is optimized (Charnov 1976; Elliott, Davoren & Gaston 2008). One model that has been widely used to describe this theory of optimal foraging is the marginal value theorem (MVT), which is used to predict how much time an animal should spend in exploiting a food resource in a patch before moving on to the next patch or returning to the nest (Charnov 1976). Since the animal will spend some time in the patch, it has to make decisions on which patch to visit, where to search, which food types to eat and when to leave (Charnov 1976; Pyke, Pulliam & Charnov 1977). Ideally they should search for prey that provide the greatest energy benefit for survival and reproductive success, while the time spent obtaining these resources is minimized (Schoener 1971; Pyke 1984). Successful foragers are favoured by natural selection, which leads to animals foraging in such a way that they optimize their energy gain and, accordingly, maximize their fitness (Stearns 1992).

Following the MVT, the animal's rate of energy extraction is initially high when a foraging patch is entered. The animal is expected to acquire food fairly quickly at first, so there will be a roughly linear relationship between food gain and time spent exploiting the foraging patch. However, as the foraging patch is exploited, the rate of energy gain is expected to gradually decline with time as the patch becomes depleted. Thus, the amount of energy (marginal value) of the patch declines (Stephens 2008). If the patch is abandoned too rapidly, energy gain is expected to be low. On the other hand, if the time spent in the patch is too long, more food will be gained in total, but the overall rate of energy extraction will not be optimized and the capture rate in the

patch is expected to decline with increasing time spent in the patch. Patch depletion will therefore eventually force an animal to move. The MVT predicts that the optimal foraging time is achieved when the maximum net rate of energy intake equals the long-term average rate of gain in the patch. Thereafter the animal should move to another patch to continue foraging in more profitable patches (Charnov 1976). Furthermore, the optimization of the rate of resource gain also depends on the costs of travelling to each patch. Generally, long travelling time to the patch requires a higher optimum energy gain than short travelling time due to the higher energetic costs of travel, and the time spent in the patch should be longer than when the travelling time is short (Stephens 2008). However, as demonstrated by a number of studies, this also depends on the quality of the foraging patch (Nonacs 2001; Halsey & Butler 2006; Burke & Montevocchi 2009; Hamilton 2010). When several patches of varying quality are encountered, the animal should bias its foraging efforts such that eventually all patches are exploited to an equal prey density (Nonacs 2001). Therefore, patches with a prey density lower than the average should be abandoned sooner than patches with high prey density.

The MVT applies only to foraging in a patchy habitat, where food is found in discrete patches separated with areas with no resources so that the animals must spend time travelling between patches. Following this, three assumptions regarding MVT are defined; (1) while an animal is foraging in a patch and depletes the amount of resources within this patch, its rate of food intake for that patch gradually decreases with time spent there, i.e. the animal experiences a diminishing return, (2) the habitat is assumed to be composed of different patch types distributed randomly throughout the habitat, and separated by distances across which the animal must travel, (3) the animal is assumed to make decisions on when to leave the patch in order to optimize the net rate of energy intake during a foraging bout (Charnov 1976).

Stephens and Krebs (1986) and Nonacs (2001) reviewed several empirical studies that have provided good support for the MVT hypotheses, although most of these studies were performed under controlled conditions. The studies typically involved animals that were provided with artificial food patches of variable quality and on different locations, both in captivity and in the wild. The outcome of the studies typically showed that rich food patches were preferred over



poor food patches and patch residence time increased with patch quality (Stephens & Krebs 1986). For instance, a study on foraging behaviour of great tits *Parus major*, where artificial food patches with hidden mealworms were established, found a positive relationship between travel time and foraging time, supporting the predictions of the MVT (Cowie 1977). Also, several studies on Eastern chipmunks *Tamias striatus* confirmed the positive relationship between food load size and distance to the foraging site. Chipmunks carry food items in their cheek pouches and transport them back to their burrows where they are stored for later consumption. An increasing travelling time to the foraging site resulted in a larger food load brought back to the burrow (Giraldeau & Kramer 1982; McAleer & Giraldeau 2006). Kacelnik (1984) tested the predictions of the MVT on starlings *Sturnus vulgaris* by providing mealworms at increasing time intervals and at varying distances to the nest. An increasing load size with increasing distance to the nest was found, which confirmed the assumption of diminishing returns. In this study, also load sizes corresponded with those predicted by the MVT. A recent study by Watanabe, Ito and Takahashi (2014) provided good qualitative support for the MVT in a natural predator-prey system. The capture rate of krill by Adélie penguins diminished with time spent foraging, and the patch residence time increased when they foraged in a high quality patch.

Many studies also do not meet the predictions from the MVT. A study by Ford *et al.* (2015) on Adélie penguins did not find good support of the theory as the capture rate of prey did not decline with time spent in the foraging area. Furthermore, foraging effort also seemed to be higher closer to the colony. Nonacs (2001) reviewed 26 studies and found that the majority of them did not meet the predictions from the MVT. Most animals stayed longer in the patch than the predicted optimal time. Nonacs (2001) suggested that the deviations from the MVT may be a result of state-dependent behaviour. For instance, it is reasonable to assume that animals are performing several activities in the foraging area than just searching for food, e.g. check for potential predators and search for mating opportunities. Besides, animals vary regarding to hunger states, energy reserves and parental demands. Also, environmental conditions can vary over time, influencing the overall patch quality over time. These factors are not included in the MVT (Nonacs 2001).

Seabirds are long-lived species, and biparental care, occurring in more than 90% of the species (Lack 1968), is essential for their reproductive success. Several studies on daily time budgets during chick rearing have demonstrated that activities of adult seabirds can be divided into four categories: foraging, flying, resting at the sea surface/in the foraging area and time spent in the colony (Cairns, Bredin & Montevecchi 1987; Wanless, Harris & Morris 1995; Daunt *et al.* 2002; Tremblay, Cook & Cherel 2005; Chivers *et al.* 2012). Studies on seabird foraging ecology are often restricted to the breeding season when parents are expected to increase their food provisioning in response to the increasing energy needs of the chicks as they grow older (Shealer 2002). During this period, parents are expected to optimally allocate their resources between sustaining themselves and their chicks (Chaurand & Weimerskirch 1994; Ydenberg *et al.* 1994; Phillips *et al.* 2004; Burke & Montevecchi 2009; McLeay *et al.* 2009). Wanless, Harris and Russell (1993) showed that European shags *Phalacrocorax aristotelis* brought back heavier food loads with increasing distance from the breeding colony. Also, the food load brought back to the nest was heavier when the chicks were larger. The breeding performance of the shag is closely related to the availability of food and their individual foraging performance (Grémillet *et al.* 2004b; Daunt *et al.* 2007). When the abundance of food is low, breeding success also tends to be lower (Rindorf, Wanless & Harris 2000; Lorentsen *et al.* 2015). Therefore, it is important that shags optimize their foraging efficiency, especially during breeding season.

The European shag (hereafter 'shag') is a colonial central-place forager that feeds on a variety of fish species found around the colony. In this study, the shag was used as a model species in order to investigate how parents adjust their foraging behaviour during the chick rearing period, in response to the increasing energy needs of their chicks. The overall objective was to investigate which factors influence the variation among individuals in foraging behaviour, which included time spent diving (i.e. searching and hunting for food) and resting, as well as the number of foraging patches visited during a foraging trip. Based on the MVT it was predicted that adults would spend more time in a foraging patch when the distance to the colony increased. It was also expected that they would spend more time diving when they were foraging further away from

the colony. Due to longer flying times with increasing distance from the colony, the third prediction was that the time spent resting in the foraging patch would also increase in order to recover from the increased travelling costs. Finally, the fourth prediction was that shags would visit more sub-patches when further away from the colony. Given the predictions above, combined with the increasing energy needs of their chicks and assuming that the patch quality is fairly constant, it is hypothesised that more patches are visited when further away from the colony in order to obtain the optimal energy gain to provide for themselves and their chicks. Furthermore, because shags show sexual size dimorphism, males and females may respond differently to the MVT. Therefore, this study also investigated whether inter-sexual differences were present in different measures of foraging activity (for instance time spent in foraging patch, time spent diving, diving depth etc).



# Materials and methods

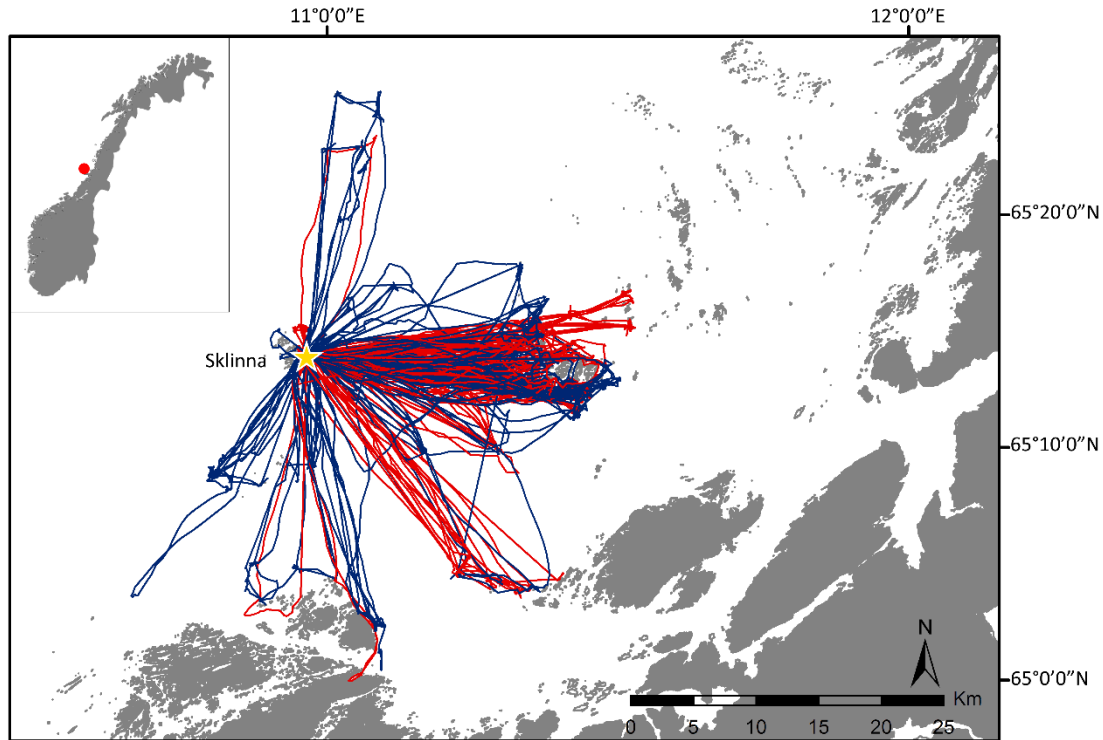
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## STUDY SPECIES

The European shag is widely distributed along the European coasts of the North Atlantic Ocean and the Barents Sea, and along the coasts of North Africa, the Mediterranean and the Black Sea (Nelson 2005). It is a medium-sized, dimorphic seabird with an average body mass of  $1897 \pm 145.72$  g for males and  $1597 \pm 88.32$  g for females in the study population. European shags mainly breed along rocky shores, and build their nest in cavities under rocks and open ledges on craggy cliffs (Røv, Tatarinkova & Paneva 2000; Velando & Freire 2003). A clutch of 2-5 eggs is laid in May, and chicks hatch one month later, being completely reliant on their parents for shelter and food. Chicks are fledged at the age of about 50 days (Velando & Freire 2003) and sexual maturity is reached at the age of 2 years (Crawford & Dyer 1996). Shags are typical coastal, foot-propelled divers which feed on benthic and pelagic fish (Cooper 1986; Wanless *et al.* 1997a; Grémillet *et al.* 1998). The diet consists mainly of sandeel, saithe and cod (Harris & Wanless 1993; Grémillet *et al.* 1998; Barrett *et al.* 2002; Velando, Munilla & Leyenda 2005; Hillersøy & Lorentsen 2012). At Sklinna, saithe of the first three age-classes is the preferred prey (Hillersøy & Lorentsen 2012; Lorentsen *et al.* 2015), and this prey is mainly obtained from kelp forested areas (S.-H. Lorentsen unpubl.). Shags quickly handle and swallow their prey under water during diving, however larger prey may lead to an interruption of the dive since they require a longer handling time (Grémillet *et al.* 1998). Cormorant species, including shags, have a wettable plumage and have to dry their wings and plumage after foraging (Grémillet, Tuschy & Kierspel 1998; Grémillet *et al.* 2005). During the chick rearing period, parents make alternate foraging trips during the day, on average two trips per adult (Wanless, Grémillet & Harris 1998).

## STUDY AREA

Data were collected at Sklinna, a small archipelago about 20 km off the coast of Nord-Trøndelag, Central Norway (65°12'N 10°59'E), covering an area of 589 ha, including 106 ha of land (Fig. 1). The archipelago consists of several islands divided by shallow water (Ramsar 2012). The study population was located on the breakwater between the islands Heimøya and Hansholmen. Sklinna has been an important site for seabird monitoring since the early 1980s. It was established as a SEAPOP (Seabird Populations – a Norwegian monitoring programme for seabird populations) key-site in 2007 (Lorentsen, Moe & Stübner 2010) and was designated as a Ramsar site in November 2010 (Ramsar 2012). Sklinna is an important breeding site for seabirds, with 20.000-25.000 individuals during early summer, where the most numerous species in the archipelago are the European shag, great cormorant *Phalacrocorax carbo*, Atlantic puffin *Fratercula arctica*, Common Guillemot *Uria aalge*, and Black Guillemot *Cephus grylle* (Ramsar 2012). Sklinna has one of the world's largest colonies of shags and is one of Norway's most important breeding sites (Hillersøy & Lorentsen 2012). During 1984-2015 the population of European shag has increased by 4.4% annually, counting 2200 breeding pairs in 2015 (S.-H. Lorentsen pers comm).



**Fig. 1.** Map of the study site Sklinna in central Norway, including the GPS tracks from 112 foraging trips from 16 males (blue) and 16 females (red). Data were collected in June and July 2013.

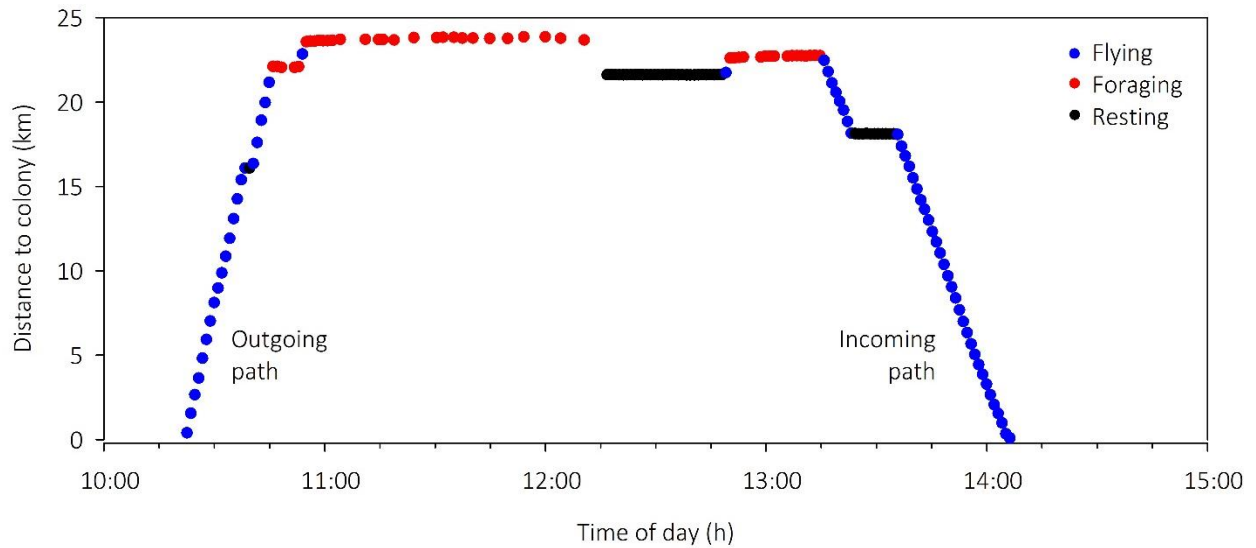
## DATA COLLECTION

Field work was conducted during chick-rearing in June-July 2013. At least one adult shag is normally present at the nest site during the chick-rearing period, when parents make alternate foraging trips (Wanless, Grémillet & Harris 1998). Nests were randomly selected from the colony. Adults were captured at their nesting sites using a pole and noose or, when possible, by hand. Each bird was captured twice; once to deploy the loggers and a second time to retrieve the loggers. Two data-loggers were deployed on each bird: one GPS logger (Global Positioning System, i-gotU GT-120, Mobile Action Technology) and one TDR (Time Depth Recorder, G5, CEFAS Technology). The GPS logger recorded geographical positions of the shag every 60 seconds, whereas the TDR recorded time and depth of each dive at 1 second intervals. All GPS loggers were disassembled from their external case and re-housed in a heat-shrink tube to ensure a

watertight seal. To save time during deployment, the TDR was attached to one side of the GPS logger using TESA® tape before deployment. The total package weighed in average  $30.6 \pm 0.3$  g, corresponding to 1.6% and 1.8% of the mean body mass of males and females, respectively. Upon deployment the loggers were attached to the middle tail feathers using strips of TESA® tape, and the shags were released as close to the nest as possible. The handling time during deployment averaged  $3.7 \pm 1.3$  min. At the time of deployment and retrieval, the chicks were weighed using Pesola spring balances (accuracy of  $\pm 2$  g for chicks less than 100 g,  $\pm 5$  g for chicks between 500 and 1000 g and  $\pm 10$  g for chicks less than 2500 g) and immediately released back to the nest. Both GPS and TDR data were recorded for approximately 3 days, after which the adults were re-caught, loggers were removed and the data was downloaded. Where possible, both parents were instrumented. Some loggers (28% of those deployed) could not be retrieved as some birds lost their loggers or abandoned their nest when chicks died or after it got predated and therefore could not be recaptured. The time used for handling the adult during retrieval of the loggers averaged  $8.4 \pm 2.6$  min.

All recorded GPS-tracks from completed foraging trips were mapped into GIS (ArcMap 10.1) to confirm the foraging area designations (Fig. 1). GPS positions  $\geq 300$  m away from the nest site were considered as foraging trip. GPS data were examined in order to identify the foraging patches and to categorize all locations according to behaviour during a foraging trip. GPS locations with speed  $> 3 \text{ m s}^{-1}$  were identified as flying birds travelling from the colony to the foraging patches and travelling between sub-patches (Quintana *et al.* 2011). This was confirmed by visual inspection of the GPS data (Fig. 2). A foraging patch was defined as an area explored for foraging by an individual during a foraging trip. Within each foraging patch, a bird was able to visit several sub-patches, as is indicated by the red dots in Fig. 2.





**Fig. 2.** Example of the GPS data from a foraging trip. Blue dots indicate the GPS positions expressed as distance from to the nest vs. time of the day during a foraging trip. Red dots indicate the period spent foraging in a sub-patch and black dots indicate the time spent resting.

Time-depth data were retrieved and classified with the software package MultiTrace Dive Analysis (Jensen Software Systems). Dives of  $\geq 0.5$  m were considered as proper dives and used for further analyses. Some individuals stayed overnight in the feeding area during a foraging trip. These trips were excluded from the analyses. Due to limited battery capacity, some foraging trips were not recorded completely and were therefore also removed from further analyses.

In total, 32 loggers from 16 males and 16 females were retrieved. Data were recorded for 112 foraging trips and used for further analyses. Samples included males and females with different numbers of chicks and with varying ages of chicks (see Table 1 for sample sizes).

**Table 1.** Sample sizes of European shag parents and the number of foraging trips distributed among a) parental sex and b) clutch sizes.

		Sample size	Number of foraging trips
a) Sex	Males	16	56
	Females	16	56
	Total	32	112
b) Clutch sizes	1 chick	7	18
	2 chicks	18	69
	3 chicks	7	25
	Total	32	112

By reducing the handling time of each bird as much as possible at the initial catch and instrumentation, stress was avoided and the probability of re-catching was increased to nearly 100 % (S.-H. Lorentsen pers. comm.). All handling of the birds were in accordance with Norwegian regulations, and approved by the Animal Research Authorities.

## DATA ANALYSIS

Statistical analyses were performed in the statistical software R, version 3.0.2 (R Development Core Team 2013). For all analyses, generalized linear mixed models (GLMM) fitted by residual maximum-likelihood (REML) were performed using the R package lme4 (Bates *et al.* 2014), with a Gaussian distribution to analyse continuous data, and a Poisson distribution to analyse count data. To account for the interdependence of repeated measurements of the same individuals and, thus, avoiding pseudo-replication, individual parent identity was included as a random variable in all models. To account for potential correlation of partner behaviour during chick rearing, nest site was included as a second random variable in all models.

To investigate the differences in foraging trip characteristics between males and females, each of the focal response variables that were derived from the data loggers (see Appendix S1) were included in separate analyses with parental sex as a fixed factor.

The analyses of the individual variation in foraging behaviour were divided in four sections according to the different activities that shags perform while in the foraging patch, including (1) time spent in the foraging patch, (2) time spent diving, (3) time spent resting and (4) number of sub-patches visited. The residual error distribution of the response variables 1, 2 and 3 were checked for normality by using the Shapiro-Wilk test and transformed when necessary. When analysing the number of foraging patches visited, a Poisson error distribution was applied. Candidate models were composed using the same explanatory variables in all models, including (a) distance to the colony, (b) clutch mass, (c) clutch size and (d) parental sex. In addition, an interaction between sex and each of the explanatory variables was included in the models because foraging behaviour can vary between the sexes. Models included one interaction only, and an interaction between two variables was only included when the respective variables were present as main factors. To account for multicollinearity within the analyses, the correlation between the explanatory variables were tested (Appendix S2) and highly correlated variables ( $r > 0.5$ ), if found, were not accepted within the same model. Effects of explanatory variables were considered significant if their 95% confidence interval did not overlap zero.

To select the most parsimonious model, all candidate models were ranked according to the Akaike Information Criterion corrected for small sample size ( $AIC_c$ ) based on the model's maximum likelihood (ML) (Burnham & Anderson 2002). The model with the lowest  $AIC_c$  was assumed to be the best model and was used for further statistical analyses. However, models with a  $\Delta AIC_c \leq 2$  relative to the highest ranked model were considered to be equally good. In that case, the most parsimonious model, i.e. the model with the fewest parameters, was preferred. Furthermore, the Akaike weight ( $wAIC_c$ ) was examined, which indicated the probability that the model was the best among the whole set of candidate models (see Appendix S3 for the whole set of models that were run for all analyses). The candidate models were composed based on sound biological foundation. Due to the restricted sample size, simple structured models were composed to avoid the problem of overfitting (Burnham & Anderson 2002).

One of the central assumptions underlying the MVT is that an animal experiences a diminishing return while foraging in a patch. Accordingly, it could be hypothesized that, as the patch becomes

depleted, the longer time individuals should spend under water to catch prey. Thus, diving performance was analysed by using dive duration per dive as a proxy for prey acquisition. Dive duration per dive was set as a response variable, with bout duration and parental sex as fixed factors, and individual identity as a random factor. Dive duration per dive was defined as the time spent underwater during one dive. Bout duration was defined as the duration of a series of dives, including time spent diving and surface time between consecutive dives, i.e. a period of diving activity between two long surface intervals. To control for the effect of descent and ascent duration, diving depth was also included in the model as a fixed factor (Watanabe, Ito & Takahashi 2014). A second order term of bout duration was added to account for a non-linear effect (i.e. 'the diminishing return-effect'), and an interaction between sex and bout duration was included to investigate possible intersexual differences in the shape of the relationships. For this analysis, a sample of the TDR data was used by selecting the first longest bout in the first patch visited during the first foraging trip sampled for each individual. This was done in order to avoid the foraging behaviour being affected by previous trips during the sample period.

# Results

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## GENERAL FORAGING BEHAVIOUR AND INTER-SEXUAL DIFFERENCES

The average number of foraging trips per day for males and females was  $1.68 \pm 0.10$  SE and  $1.80 \pm 0.14$  respectively ( $P = 0.41$ ). Foraging activity occurred throughout the day, mainly between 05:00 and 21:00 h. Shags used a large variety of foraging patches, most of them characterized as kelp forested areas (S.-H. Lorentsen unpubl.) (Fig. 1). Most individuals used the same area on multiple foraging trips, although some individuals went to different areas. An archipelago about 20 km east of Sklinna, was the main foraging patch for both males and females. In addition, some males also went foraging north and south of Sklinna, while females used an additional area in the south-eastern direction. During a foraging trip shags performed either a direct return trip, where they went straight to a particular patch to forage and then returned to the colony following the same path or occasionally a path parallel to the outward route, or a loop-shaped trip. Birds alternated periods of flight with periods of diving (presumed foraging), swimming between consecutive dives and resting. Once foraging activities had been concluded, shags returned directly to the colony executing either non-stop flight or interspacing flight periods with a short stop. The average trip length, mean- and maximum distances to the colony, time spent in the foraging patch and number of sub-patches visited during a foraging trip did not differ between males and females (Table 2). However, several diving parameters differed significantly between the sexes (Table 2). The average duration of dives for males was almost twice as long as for females, but males made ca. 40% fewer dives per trip as females. Also, males dived almost twice as deep as females and their post-dive interval was much higher than for females (see Appendix S4). However, the total time spent diving, the total bottom time during a foraging trip and the dive efficiency did not differ significantly between males and females.

**Table 2.** Parameter estimates for foraging trip characteristics for male and female European shags during chick rearing period at Sklinna, Norway 2013. Means are given with 95% CI. Also the difference between males and females ( $\beta$ ) is given with 95% CI. Statistically significant differences between males and females (95% CI does not include 0) are shown in bold. All parameter estimates are given per foraging trip. n=number of trips included in the analyses.

Foraging trip characteristics	Males (n=56)			Females (n=56)			$\beta$	95% CI	
	Mean	95% CI		Mean	95% CI			Lower	Upper
		Lower	Upper		Lower	Upper			
Trip duration (min)	224.06	199.74	248.37	222.35	197.98	246.73	-1.70	-36.13	32.72
Time in foraging patch (min)	171.98	150.26	193.71	171.82	150.04	193.59	-0.17	-30.93	30.59
Trip length (km)	42.84	37.89	47.79	43.29	38.33	48.25	0.45	-6.56	7.45
Distance to colony (km)	17.90	15.75	20.05	18.74	16.59	20.89	0.84	-2.20	3.88
Maximum distance to colony (km)	19.09	16.84	21.28	19.76	17.53	21.99	0.70	-2.44	3.84
Total diving time (min)	71.57	62.37	80.78	69.29	60.06	78.51	-2.28	-15.32	10.75
Diving duration per dive (sec)	60.34	50.67	70.01	32.17	22.49	41.86	<b>-28.18</b>	<b>-41.85</b>	<b>-14.48</b>
Total bottom time (min)	28.27	23.34	33.29	30.85	25.91	35.79	2.59	-4.39	9.56
Bottom time per dive (sec)	21.72	19.73	23.70	14.08	12.09	16.07	<b>-7.64</b>	<b>-10.45</b>	<b>-4.83</b>
Diving depth (m)	11.67	10.03	13.32	6.06	3.28	7.71	<b>-5.61</b>	<b>-7.94</b>	<b>-3.28</b>
Maximum diving depth (m)	33.51	29.28	37.73	19.34	15.11	23.57	<b>-14.16</b>	<b>-20.14</b>	<b>-8.18</b>
Bottom depth (m)	17.80	14.35	21.24	8.48	5.02	11.93	<b>-9.32</b>	<b>-14.20</b>	<b>-4.44</b>
No. of dives	84.21	64.26	104.17	137.19	117.17	157.21	<b>52.97</b>	<b>24.71</b>	<b>81.24</b>
Total pause (min)	43.87	38.28	49.45	40.50	34.91	46.10	-3.37	-11.27	4.54
Post dive interval (sec)	37.94	30.49	45.39	20.33	12.87	27.78	<b>-17.61</b>	<b>-28.15</b>	<b>-3.28</b>
Dive efficiency	0.25	0.22	0.29	0.27	0.24	0.30	0.02	-0.02	0.05
Bout duration (min)	114.83	101.04	128.62	109.54	95.72	123.35	-5.29	-24.82	14.23
No. of bouts	2.31	2.00	2.63	2.32	2.00	2.63	0.004	-0.44	0.45
Resting time (min)	51.14	37.42	64.89	56.64	42.86	70.41	5.49	-13.96	24.93
No. of sub-patches visited	1.59	1.30	1.88	1.73	1.44	2.02	0.14	-0.27	0.55

The allocation of time while in the foraging patch indicated that males and females spent approximately equal times to different activities (Table 3). About 40% of the time was spent diving (presumed foraging) and about 25% of the time was spent swimming on the surface between the dives. The rest of the time was spent resting. A very small proportion of the time spent in the feeding area was spent on flying between different sub-patches.

**Table 3.** Time spent in the foraging patch (mean  $\pm$  SE, along with minima and maxima) and time allocation (%) in the foraging patch during a foraging trip. Males: 56 trips from 16 individual males. Females: 56 trips from 16 individual females.

	Time in foraging (min)	Proportion (%) of time in foraging patch spent			
		Diving	Swimming	Resting	Flying
Males	171.98 $\pm$ 10.52 (36.68-369.58)	41.62	25.51	29.74	3.14
Females	171.82 $\pm$ 9.67 (54.87-320.27)	40.33	23.57	32.96	3.14

## TIME SPENT IN THE FORAGING PATCH

Variation in the time spent in the foraging patch was best explained by distance to the colony, clutch mass, parental sex and the interaction between distance to the colony and parental sex (Table 4a, model F1). Distance between the colony and the foraging patch had a positive effect on the time spent in the foraging patch, indicating that the time spent in the foraging patch increased significantly with increasing distance to the colony. This positive effect was more pronounced for males than for females. However, less time was spent in the foraging patch when the clutch mass was larger (Table 5a). According to the  $AIC_c$  ranking, all the other candidate models received less support compared to model F1 ( $\Delta AIC_c > 2$ , Table 4a). The most parsimonious model was also supported by a strong  $AIC_c$  weight ( $wAIC_c$ ), indicating that model F1 had a probability of 66% to be the best model, given the candidate models and the data.

## TIME SPENT DIVING

Variation in the total time spent diving during a foraging trip was best explained by a model that included distance to the colony, parental sex and the interaction between those parameters (Table 4b, model D1). The model was accompanied by an  $AIC_c$  weight of 0.57, indicating a high support for the highest ranked model, given the candidate models and the data. Males increased their total time spent diving with increasing distance to the colony, while females spent less time diving when further away from the colony (Table 5b). The second best model, which had an  $AIC_c$  value of 1.29 units higher than the top ranked model and therefore could be considered equally good ( $\Delta AIC_c \leq 2$ ), included also clutch mass. Analysis indicated that there was a tendency for clutch mass to have a negative effect on time spent diving, but this effect was not significant ( $\beta = -0.0001$ ;  $CI = [-0.0003, 0.0001]$ ).



## TIME SPENT RESTING

The analysis of factors that influenced the variation in time spent resting resulted in three models with  $\Delta AIC_c \leq 2$  (Table 4c, Model R1, R2, and R3). Among those three models, model R1 was the most parsimonious model according to the  $AIC_c$  values and received relatively high support from the data ( $wAIC_c = 0.26$ ) compared to the other models. Variation in the total time spent resting during a foraging trip was best explained by distance to the colony and clutch mass. When further away from the colony, the time spent resting increased. However, when broods were larger, the resting time in the foraging patch decreased and caused the parents to return to the colony more rapidly (Table 5c). Models following the top ranked model according to  $AIC_c$  included also parental sex and an interaction between parental sex and either distance to the colony (R2) or clutch mass (R3). However, even though these received relatively high support from the data compared to model R1, analyses showed that these parameters did not have a significant effect on the time spent resting.

## NUMBER OF SUB-PATCHES VISITED

For the number of sub-patches during a foraging trip, four models received equal support according to the  $AIC_c$  values (Table 4d, Model P1, P2, P3 and P4,  $\Delta AIC_c \leq 2$ ). The top-ranked model (Model P1) was used for further analysis. According to this model, the number of sub-patches was best explained by distance to the colony and clutch mass (Table 5d). Analysis showed that there was a tendency for an increasing number of sub-patches visited during a foraging trip when distance to the colony increased, however, this was not significant. The number of sub-patches visited during a trip decreased when the clutch mass was larger.

**Table 4.** The 5 highest ranked models out of 30 candidate models according to the AIC<sub>c</sub> criteria describing the individual variation in a) time spent in the foraging patch, b) time spent diving, c) time spent resting and d) number of sub-patches visited during a foraging trip in a population of breeding European shags at Sklinna, Norway (see Appendix S3 for the complete sets of candidate models). Models were constructed using square root transformed time in feeding area (F) as a function of average distance to the colony (DC), clutch mass (CM), clutch size (CS), parental sex and parental sex interacting with distance to the colony, clutch mass and clutch size and clutch mass interacting with clutch size (interactions are indicated with a colon). Also the number of parameters in each model (K), Akaike Information Criterion corrected for small samples (AIC<sub>c</sub>) scores, the difference from the top-ranked model ( $\Delta AIC_c$ ) and AIC<sub>c</sub> weight (wAIC<sub>c</sub>) are shown.

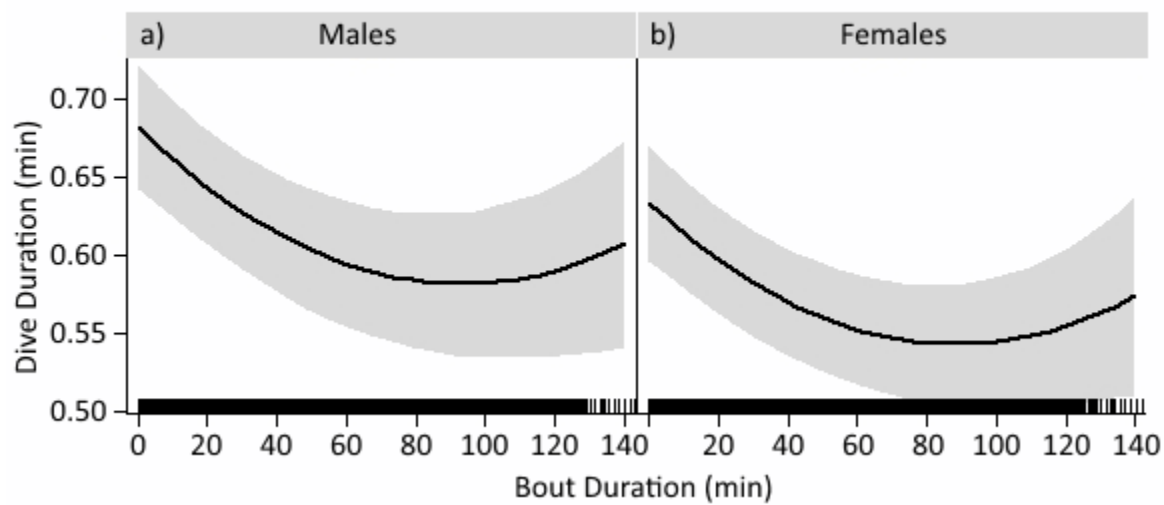
Rank	Variables	K	AIC <sub>c</sub>	$\Delta AIC_c$	wAIC <sub>c</sub>
a) Time spent in foraging patch					
F1	DC + CM + Sex + DC:Sex	8	551.71	0.00	0.66
F2	DC + CM + CS + Sex + DC:Sex	10	554.42	2.71	0.17
F3	DC + DC:Sex	7	557.39	5.67	0.04
F4	DC + CM	6	558.43	6.72	0.02
F5	DC + CM + Sex + CM:Sex	8	558.46	6.74	0.02
b) Time spent diving					
D1	DC + Sex + DC:Sex	7	140.85	0.00	0.57
D2	DC + CM + Sex + DC:Sex	8	142.14	1.29	0.30
D3	DC + CS + DC:Sex	9	145.00	4.16	0.07
D4	DC + CM + CS + Sex + DC:Sex	10	146.52	5.68	0.03
D5	Intercept only	4	149.01	8.16	0.01
c) Time spent resting					
R1	DC + CM	6	582.41	0.00	0.26
R2	DC + CM + Sex + DC:Sex	8	583.46	1.05	0.16
R3	DC + CM + Sex + CM:Sex	8	584.01	1.60	0.12
R4	DC + CM + Sex	7	584.47	2.06	0.09
R5	DC + CM + CS + Sex	8	584.63	2.23	0.09
d) Number of sub-patches visited					
P1	DC + CM	5	315.93	0.00	0.22
P2	CM	4	316.78	0.85	0.15
P3	Intercept only	3	317.27	1.34	0.11
P4	DC	4	317.84	1.90	0.09
P5	DC + CM + Sex	6	318.09	2.16	0.08

**Table 5.** Parameter estimates for the model best explaining the individual variation in a) time spent in feeding area, b) time spent diving, c) time spent resting and d) number of sub-patches visited during a foraging trip in a population of breeding European shags at Sklinna, Norway. The explanatory variables include average distance to the colony (DC), clutch mass (CM), parental sex and parental sex interacting with distance to the colony (interactions are indicated with a colon).  $\beta$  is the parameter estimate. The uncertainty of the estimates is given by its 95% confidence interval (CI). Effects of the parameters were considered significant if their 95% CI did not include 0.

Variables	$\beta$	95% CI	
		Lower limit	Upper limit
a) Time spent in foraging patch			
Intercept	7.752	5.178	10.325
DC	0.355	0.208	0.501
CM	-0.002	-0.004	-0.001
Sex2 (female)	6.129	2.336	9.922
DC:Sex2	-0.348	-0.550	-0.145
b) Time spent diving			
Intercept	3.716	3.297	4.135
DC	0.026	0.003	0.049
Sex2 (female)	1.131	0.515	1.747
DC:Sex2	-0.065	-0.097	-0.032
c) Time spent resting			
Intercept	2.111	-0.044	4.267
DC	0.302	0.184	0.420
CM	-0.002	-0.004	$-2.7 \times 10^{-4}$
d) Number of sub-patches visited			
Intercept	0.236	-0.371	0.842
DC	0.028	-0.005	0.060
CM	$-4.4 \times 10^{-4}$	-0.001	$-4.9 \times 10^{-6}$

## DIVING PERFORMANCE

After controlling for the negative effect of diving depth ( $\beta = 0.041$ ; CI = [0.039, 0.042]), the analysis of diving performance showed that there was a negative relationship between dive duration and bout duration for males ( $\beta = -0.002$ ; CI = [-0.003, -0.001], Fig. 3a), and the slope for females (Fig. 3b) did not differ significantly from the slope of males ( $\beta = -0.0001$ ; CI = [-0.0004, 0.0006]). The average dive duration did not differ significantly among the sexes.



**Fig. 3.** Relationship between dive duration per dive and bout duration for a) males and b) females.

# Discussion

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## GENERAL FINDINGS

This study has demonstrated the presence of intersexual differences in foraging behaviour of European shags in a colony in central Norway, and which factors influence individual variation in foraging behaviour. As predicted by the MVT, distance to the colony was an important predictor of both the variation in time spent in the foraging patch and time spent diving, as well as time spent resting. The time spent in the foraging patch increased with increasing distance to the colony, especially for males. This corresponds to the predictions of the MVT, where individuals should maximize their foraging efficiency during a trip in order to optimize their energy intake. Foraging further away from the colony also had a positive effect on time spent diving in males, whereas it had a negative effect on time spent diving in females. This would suggest that the sexes respond differently to the MVT, as it predicts that more time should be spent foraging when the distance to the colony increases. However, trip durations and distances, and total diving time per trip did not differ between males and females, which indicated that they did not respond differently to the predictions of the MVT, but instead have different foraging strategies, which was especially found in their diving behaviour. Males dived for a longer time and much deeper than females, while females made more dives than males. Furthermore, the time spent resting in the foraging area increased with distance from the colony, but clutch mass had a negative effect on the time spent resting, suggesting that the parents devoted a larger proportion of their time in the foraging area to prey acquisition as their chicks grew older. Also, parents visited less sub-patches when chicks grew bigger, suggesting that parents foraged more intensely in fewer sub-patches when the clutch mass increased. Assuming that dive time is positively correlated with prey acquisition, the shags did not experience a diminishing return while foraging, which is an important assumption of the MVT.

## MVT ASSUMPTIONS

Three assumptions apply to the MVT (Charnov 1976). The first one assumes that the rate of food intake decreases over time. Measuring the energy intake of animals foraging in the open ocean is difficult due to limited knowledge about the quality, distribution, abundance and behaviour of their potential prey (Hindell 2008). Also, information on successful prey capture is often lacking. In the present study, individual dive durations were used as a proxy for prey acquisition, and was used in a simple model to estimate the diving performance, and thus, food intake, for male and female shags. Assuming that the dive time is positively correlated with prey acquisition, the findings in this study did not support the hypothesis of diminishing return. This could be explained by several hypotheses. When shags arrive in the foraging patch, they may start foraging at the outskirts of the patch often consisting of kelp forested areas, where water is deeper and, hence, results in longer dive durations. During these foraging activities, the targeted fish is expected to move towards the kelp forests to seek shelter (S.-H. Lorentsen pers. comm.). Accordingly, shags will follow the prey and continue foraging in the more shallow kelp forested areas as the diving bout progresses. If so, it might be adaptive to start in the deeper open water, which explains the longer dive durations at the beginning of a bout, and then move to the shallow areas resulting in shorter dive times. Furthermore, the shag's stomach is filling up with time in the patch. The amount of prey fed to the chicks after each trip (assuming 2 trips per adult per day) corresponds to up to about 10% of the shags body mass (Grémillet *et al.* 1996). This may eventually slow them down during diving and result in more shallow dives and reduced prey capture over time. Furthermore, diving is energetically costly and birds may run out of oxygen more quickly towards the end of the bout. It is assumed that foraging in between the kelp forest is more energy and time consuming than foraging above the kelp canopy or in open water, forcing them to start hunting deep at the beginning of the bout, and forage more and more shallow as the bout progresses.

Following the findings in this study, one could also question the assumption whether shags always experience a diminishing return when foraging. This assumption is supposed to be valid for prey that don't move, or move very slowly compared to the predator's speed of prey acquisition, for example eastern chipmunks foraging on sunflower seeds (Giraldeau & Kramer

1982; McAleer & Giraldeau 2006), or great tits and starlings foraging on mealworms (Cowie 1977; Kacelnik 1984). Shags hunt on fast swimming fish that is expected to move as fast as they do. Therefore, they face the challenge of foraging in patches where prey escapes. In this study we only had access to data collected by GPS and TDR, which do not give any insight in patch quality and food intake rates. Generally, it is difficult to quantify available food resources in kelp forested areas (but see Lorentsen, Sjøtun & Grémillet 2010). Further studies could be done to reveal this kind of information, for example by using ROVs (e.g. Lorentsen, Sjøtun & Grémillet 2010) or animal-borne video cameras (Watanuki *et al.* 2008; Watanabe, Ito & Takahashi 2014). The second assumption from the MVT assumes that shags went foraging in sub-patches of varying quality and randomly distributed environments. In the study area, kelp-forested areas were interrupted by soft and hard bottom areas without kelp (Lorentsen, Sjøtun & Grémillet 2010; T. Bekkby, pers. comm). GPS data showed that the birds foraged in different sub-patches during a foraging trip (Fig. 1 and Fig. 2, Table 2, unpubl. data). Periods of foraging in a sub-patch were interrupted by periods of flying, assuming that they visited several foraging sub-patches before returning to their nest site. This might indicate that the birds knew when to leave a patch and travel to the next patch, in order to maximize their energy intake. Regarding theories of optimal foraging, the bird is assumed to have knowledge about the quality and distribution of foraging patches, which is the third assumption of the MVT. It is suggested that birds living in colonies exchange information about locations of favourable food patches (Ward & Zahavi 1973). In the present study, there was no data available on the variation in patch quality around Sklinna. GPS data showed that only few birds went foraging in patches close to the colony, whereas most birds went to foraging patches further way (Fig. 1). A reason for this could be that the patches close to the colony were depleted more rapidly and earlier in the breeding season, and therefore most birds went to the high quality patches that were found further away. The increasing energy demands of the chicks requires the parents to maximize their own energy intake, while the time spent obtaining food resources is minimized (Schoener 1971). Therefore they are expected to forage as close to the colony as prey conditions and energy requirements allow (McLeay *et al.* 2010). Consequently, large seabird colonies may alter the availability of prey around the colony by depleting or reducing food resources (Ashmole 1963; Birt *et al.* 1987). Also during the progress of the breeding

season, the foraging patch can expand further since the parents have to obtain food for their growing and, thus, more demanding chicks, as well as themselves (Ainley *et al.* 2004; Lyver *et al.* 2011). Furthermore, the spatial structure of the area and biological and physical features (e.g. bathymetry, sea surface temperature) could have an effect on the distribution and availability of prey (Suryan *et al.* 2006), forcing parents to forage further away from the colony.

## TIME SPENT IN THE FORAGING PATCH

Several empirical studies have tested the hypotheses following MVT using controlled experiments (Stephens & Krebs 1986; Nonacs 2001). Here, the MVT was applied to a colonial seabird. Coloniality has many benefits, including protection from predators and information exchange with conspecifics about food resources (Danchin & Wagner 1997). However, it also requires flexible, yet optimal foraging tactics to minimize constraints imposed by central place foraging. During the breeding period, central place foragers have a restricted foraging range due to the necessity of provisioning their offspring at regular intervals (Orians & Pearson 1979). This might increase the intra-specific competition for food resources within the foraging range (Furness & Birkhead 1984). Several studies suggested various mechanisms to reduce this competition. For instance, males and females may forage in different foraging patches by one sex travelling further away from the colony. This is observed, for example, in both northern *Macronectes halli* and southern *M. giganteus* giant petrels, where females foraged offshore and the males along the coast (González-Solís, Croxall & Wood 2000a; González-Solís, Croxall & Wood 2000b; Quintana, Dell’Arciprete & Copello 2010). Also in wandering albatrosses *Diomedea exulans* and blue-footed *Sula nebouxii* and brown boobies *S. leucogaster*, foraging trips of females were longer than those of males (Weimerskirch *et al.* 1993; Weimerskirch *et al.* 1997; Weimerskirch *et al.* 2009). Alternatively, both sexes travel similar distances, but exploit different foraging areas (e.g. utilize different foraging depths), which seems to be the case for the shags in the present study, and, for example, in imperial cormorants *Phalacrocorax atriceps* (Quintana *et al.* 2011). At Sklinna, a habitat utilization study performed during the same field period as the current study suggested that a variety of foraging patches was used by males and females (Fig. 1,



unpubl. data). Typically, shags flew directly from their nests to the foraging patch, performed a series of dives, rested for some time to dry their feathers and then flew back to the colony, as is also seen in other studies on shags (Wanless, Harris & Morris 1991). The duration of the time spent in a foraging patch, time spent diving and time spent resting in this study were all affected by the distance to the colony, which is in accordance to the predictions of the MVT (Charnov 1976). Shags spent more time in the foraging patch when the distance to the colony increased. Also, the time spent diving increased when further away from the colony. As Charnov (1976) suggested, individuals should maximize their foraging efficiency in order to optimize their net energy output. Accordingly, long travelling time to the foraging patch should result in a longer time spent in the foraging patch, suggesting a higher energy intake than short travelling time (Stephens 2008). In the current study, a positive relationship between time in the foraging patch and distance to the colony was found in both sexes, but was particularly pronounced (significant) for males. This is surprising, because several foraging trip characteristics, derived from GPS data, did not differ significantly between males and females, including trip duration, time spent in the foraging patch, trip length and maximum distance to the colony. This seems inconsistent with other studies on foraging behaviour of European shags. For example, a study on shags breeding at Puffin Island, Wales, Great Britain revealed a significant difference between males and females in trip duration, trip length and maximum distance travelled, with males having shorter trip durations, travelling shorter distances and staying closer to the breeding colony (Soanes *et al.* 2014). Foraging distance, direction and duration are likely to be determined by the distribution of available prey (Garthe, Montevecchi & Davoren 2007). At Sklinna, the shags' diet was dominated by young saithe of the first three-year classes (Hillersøy & Lorentsen 2012). These fish are confined to kelp forested areas (S.-H. Lorentsen pers. Comm.), which has a patchy distribution perfectly matched by the patches utilized by the shags. At the Isle of May, shags fed mainly on lesser sandeel, which is found in sandy and rocky areas around the island (Harris & Wanless 1991; Harris & Wanless 1993; Watanuki *et al.* 2008). Also, a more diverse availability and distribution of prey could explain the variation in foraging behaviour found in other colonies.

## TIME SPENT DIVING

In this study, males and females seemed to have different foraging strategies and, hence, responded differently to the predictions of the MVT. Time spent diving was positively affected by distance to the colony for males, but negatively affected for females. The MVT predicts that more energy should be obtained when foraging farther away from the colony (Charnov 1976). In total, males and females spent equal time diving during a foraging trip. However, individual diving activities differed significantly between sexes. Males dived deeper and for longer time than females, while females performed a larger number of dives (Table 2). One physiology-based functional mechanism that could explain the observed difference in diving depth and duration between sexes is related to the larger body mass in male shags, compared to females. For air breathing aquatic birds and mammals, a relationship has been found between diving capacity (depth and duration) and body size (Boyd & Croxall 1996; Schreer & Kovacs 1997; Schreer, Kovacs & O'Hara Hines 2001; Halsey, Blackburn & Butler 2006). Larger individuals are capable of diving longer than their smaller counterparts because of lower mass-specific metabolic rates, which requires less energy expenditure and therefore a slower utilization of oxygen stores (Schreer & Kovacs 1997). Many seabirds display sexual size dimorphism (Fairbairn & Shine 1993) and therefore may also show sexual differences in foraging behaviour. Several studies on seabirds have shown a relationship between diving depth and body size. Since many cormorant species are sexually dimorphic, with males larger and heavier than females, sexual differences in diving behaviour might be expected (Johnsgard 1993). This is confirmed by a study on Antarctic shags *Phalacrocorax bransfieldensis* (Casaux *et al.* 2001), and in both king- *Phalacrocorax albiventer* and Japanese cormorants *P. capillatus*, where diving depth and duration were significantly greater for males (Kato, Nishiumi & Naito 1996; Watanuki, Kato & Naito 1996; Kato *et al.* 1999). Also, male shags require a shorter recovery period after long dives compared to females (Wanless *et al.* 1993), which might explain why males dive deeper and for longer time than females. However, in a study on European shags on the Isle of May, Scotland, no significant difference in diving depth and duration was found between males and females (Wanless *et al.* 1997b). Differences in diving depth between the sexes could also reduce intra-sexual food competition, especially when foraging in the same patch. Cook *et al.* (2007) suggested that sexual differences

in diving behaviour could be an adaptation to differences in targeted prey size rather than a consequence of differences in body size. Males have higher and more powerful beaks than females and could therefore be more efficient in handling greater prey items than females.

## TIME SPENT RESTING

According to the third prediction of this study, shags would spend more time resting in the foraging area before returning to the colony. This was supported as the analyses showed that shags indeed rested for longer time when further away from the colony. However, the clutch mass negatively affected the resting time. In long-lived birds, like seabirds, parents have to make decisions on how much to invest in their current offspring in order to maximize their lifetime fitness by balancing the present and future costs and benefits of reproduction (Stearns 1992). If the foraging trip distance and/or duration increases, offspring will be fed less frequently, which may result in slower growth rates and lower body mass as fledgling (Kitaysky *et al.* 2000; Davoren & Montevecchi 2003). It may also affect the parent's body condition as longer travel distances require increased energy expenditure (Arnould *et al.* 1996). In the present study, the parents reduced the time spent resting in the foraging area in order to provide food for their aging chicks at an increasing rate. Instead of resting in the foraging area, they may have re-allocated their time budgets and moved their resting time to the period spent at the nest while their partner was out foraging, without reducing their own body condition. Furthermore, Ricklefs (1983) suggested that it is likely that adults accept energy deficits for periods of high power requirements.

## NUMBER OF SUB-PATCHES VISITED

The number of sub-patches visited by the shags in the present study was, contrary to the other variables tested, not affected by distance to the colony. Furthermore, the number of sub-patches visited decreased with increasing clutch mass, suggesting that parents forage more intensely in fewer sub-patches when their chicks are growing. Olsson, Brown and Helf (2008) suggested that

when an animal visits more than one sub-patch per foraging trip, it plans to increase its food load by visiting additional sub-patches before returning to the colony. Although a larger food load is required during the progress of the breeding season, this hypothesis was not supported by the results in this study.

## CONCLUSIONS

The present study has indicated that fundamental principles expressed in the MVT may govern allocation of foraging behaviour in European shags. Accordingly, factors that influence the optimal foraging behaviour may have severe consequences for the total energy budget and, thus, the lifetime reproductive success. In order to manage populations and implement conservation strategies successfully, it is important to have a good understanding of a species' foraging ecology and distribution (Daunt *et al.* 2002). The breeding distributions of many seabird species are associated with food availability in the vicinity of their colonies. Hence, during the breeding season, flexibility in foraging behaviour is important to ensure adequate chick provisioning to their chicks, as many marine food resources may be highly variable (Hamer *et al.* 2007). However, large fluctuations in food availability could lead to low reproductive success (Frederiksen *et al.* 2004). Shallow foraging grounds are very important for European shags and many other seabird species. But the marine environment is changing as a result of global climate change and human activities such as over-harvesting, habitat modifications and pollution (Masden *et al.* 2010). Anthropogenic activities in such ecologically important areas may have severe negative impact on population sizes over time. Disturbance and habitat loss might be of great influence on the shag's foraging behaviour, especially in the breeding period. For instance, if the shags experience reduced food availability within their foraging range, they are forced to search for other foraging patches, either by using more time to search for food in the same patch, or fly longer distances to other foraging patches. Both alternatives will presumably increase the foraging costs of the parents, which ultimately may result in lower chick survival and over time the population growth rate will decline as well (Stearns 1992).

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## Supporting information

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## APPENDIX S1: DESCRIPTION OF VARIABLES DERIVED FROM GPS AND TDR

**Table S1.1.** A description of the variables derived and calculated from the GPS and TDR data to describe the foraging behaviour of European shags.

Variable	Description
Trip duration	Total time away from the colony, starting from the moment the bird leaves the colony until it returns
Time in feeding area	Total time spent in the foraging patches, including diving, swimming, resting and flying between patches
Trip length	Total distance travelled during a foraging trip
Distance to colony	Average straight line distance from the feeding area to the colony
Maximum distance to colony	Maximum straight line distance from the feeding area to the colony
Total diving time	Total time spent underwater during a foraging trip
Diving duration per dive	Time spent underwater during one dive
Total bottom time	Total bottom time during a foraging trip
Bottom time per dive	Time spent at >80% of the maximum diving depth reached, presumed foraging (Kato <i>et al.</i> 1999)
Diving depth	Average depth of the dive
Maximum diving depth	Greatest depth of the dive
Bottom depth	Average depth of the bottom phase
No. of dives	Total number of dives during a foraging trip
Total pause	Total surface time during a foraging trip
Post dive interval	The surface period between two consecutive dives
Dive efficiency	The proportion of time that a diver spent at the bottom of a dive, thus potentially foraging, relative to the overall duration of the dive cycle, calculated as the total bottom time/(dive duration + post-dive interval) (Ydenberg & Clark 1989)
Bout duration	Duration of a series of dives, including time spent diving and surface time between consecutive dives
No. of bouts	Number of dive series (bouts) during a foraging trip
Resting time	Time spent ashore during a foraging trip, calculated as (trip duration – time spent flying – bout duration)
Number of patches	Number of foraging patches visited during a foraging trip
Clutch mass	Total mass of the brood
Clutch size	Number of chicks per nest



## APPENDIX S2: VARIABLE CORRELATIONS

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**Table S2.1.** Pearson's correlation coefficients between the explanatory variables.

	Distance to colony	Clutch mass	Clutch size	Parental sex
Distance to colony	1.00			
Clutch mass	0.28	1.00		
Clutch size	0.26	0.07	1.00	
Parental sex	0.09	-0.02	0.1	1.00

## APPENDIX S3: MODEL SELECTION

**Table S3.1.** Model selection based on AIC<sub>c</sub> explaining the individual variation in time spent in the feeding area during a foraging trip in a population of breeding European shags at Sklinna, Norway. Models were constructed using square root transformed time in feeding area (F) as a function of average distance to the colony (DC), clutch mass (CM), clutch size (CS), parental sex and parental sex interacting with distance to the colony, chick mass and clutch size and clutch mass interacting with clutch size (interactions are indicated with a colon). The number of parameters in each model (K), Akaike Information Criterion (AIC<sub>c</sub>) scores, the difference from the most parsimonious model ( $\Delta$ AIC<sub>c</sub>) and AIC<sub>c</sub> weight (wAIC<sub>c</sub>) are also shown.

Model	Int	DC	CM	CS	Sex	DC: Sex	CM: Sex	CS: Sex	CS: CM	K	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	wAIC <sub>c</sub>
F1	•	•	•		•	•	•			8	551.71	0.00	0.66
F2	•	•	•	•	•	•	•			10	554.42	2.71	0.17
F3	•	•			•	•				7	557.39	5.67	0.04
F4	•	•	•							6	558.43	6.72	0.02
F5	•	•	•		•		•			8	558.46	6.74	0.02
F6	•	•		•	•	•				9	559.43	7.72	0.01
F7	•	•	•	•						8	559.45	7.73	0.01
F8	•	•	•	•	•		•			10	559.79	8.08	0.01
F9	•	•								5	560.62	8.90	0.01
F10	•	•	•		•					7	560.65	8.94	0.01
F11	•	•		•						7	561.29	9.57	0.01
F12	•	•	•	•	•			•		11	561.29	9.58	0.01
F13	•	•	•	•	•					9	561.66	9.95	0.00
F14	•	•			•					6	562.84	11.13	0.00
F15	•	•	•	•					•	10	563.36	11.65	0.00
F16	•	•		•	•					8	563.52	11.81	0.00
F17	•	•		•	•			•		10	563.86	12.15	0.00
F18	•									4	565.22	13.50	0.00
F19	•	•	•	•	•				•	11	565.65	13.94	0.00
F20	•		•							5	565.75	14.04	0.00
F21	•		•		•		•			7	566.15	14.44	0.00
F22	•				•					5	567.34	15.62	0.00
F23	•		•		•					6	567.93	16.22	0.00
F24	•			•						6	568.12	16.41	0.00
F25	•		•	•						7	569.17	17.45	0.00
F26	•			•	•					7	570.37	18.66	0.00
F27	•		•	•	•					8	571.47	19.75	0.00
F28	•			•	•			•		9	572.63	20.91	0.00
F29	•		•	•					•	9	573.13	21.41	0.00
F30	•		•	•	•				•	10	575.52	23.81	0.00

**Table S3.2.** Model selection based on AIC<sub>c</sub> explaining the individual variation in time spent diving during a foraging trip in a population of breeding European shags at Sklinna, Norway. Models were constructed using log transformed time spent diving (D) as a function of average distance to the colony (DC), clutch mass (CM), clutch size (CS), parental sex and parental sex interacting with distance to the colony, chick mass and clutch size and clutch mass interacting with clutch size (interactions are indicated with a colon). The number of parameters in each model (K), Akaike Information Criterion (AIC<sub>c</sub>) scores, the difference from the most parsimonious model ( $\Delta$ AIC<sub>c</sub>) and AIC<sub>c</sub> weight (wAIC<sub>c</sub>) are also shown.

Model	Int	DC	CM	CS	Sex	DC: Sex	CM: Sex	CS: Sex	CS: CM	K	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	wAIC <sub>c</sub>
D1	•	•			•	•				7	140.85	0.00	0.57
D2	•	•	•		•	•				8	142.14	1.29	0.30
D3	•	•		•	•	•				9	145.00	4.16	0.07
D4	•	•	•	•	•	•				10	146.52	5.68	0.03
D5	•									4	149.01	8.16	0.01
D6	•	•								5	150.86	10.02	0.00
D7	•		•							5	151.01	10.16	0.00
D8	•				•					5	151.05	10.20	0.00
D9	•			•						6	152.26	11.41	0.00
D10	•	•			•					6	152.98	12.13	0.00
D11	•	•	•							6	153.02	12.17	0.00
D12	•		•		•					6	153.08	12.23	0.00
D13	•		•		•		•			7	153.37	12.52	0.00
D14	•			•	•					7	154.27	13.42	0.00
D15	•	•		•						7	154.41	13.56	0.00
D16	•		•	•						7	154.45	13.60	0.00
D17	•			•	•			•		9	155.07	14.23	0.00
D18	•	•	•		•					7	155.16	14.31	0.00
D19	•	•	•		•		•			8	155.43	14.58	0.00
D20	•	•		•	•					8	156.50	15.65	0.00
D21	•		•	•	•					8	156.50	15.66	0.00
D22	•	•	•	•						8	156.69	15.85	0.00
D23	•	•		•	•			•		10	157.48	16.63	0.00
D24	•	•	•	•	•					9	158.82	17.97	0.00
D25	•		•	•					•	9	159.01	18.16	0.00
D26	•	•	•	•	•		•			10	159.23	18.38	0.00
D27	•	•	•	•	•			•		11	159.89	19.04	0.00
D28	•		•	•	•				•	10	161.13	20.28	0.00
D29	•	•	•	•					•	10	161.37	20.52	0.00
D30	•	•	•	•	•				•	11	163.56	22.71	0.00

**Table S3.3.** Model selection based on AIC<sub>c</sub> explaining the individual variation in time spent resting during a foraging trip in a population of breeding European shags at Sklinna, Norway. Models were constructed using square root transformed time spent resting (R) as a function of average distance to the colony (DC), clutch mass (CM), clutch size (CS), parental sex and parental sex interacting with distance from the colony, chick mass and clutch size and clutch mass interacting with clutch size (interactions are indicated with a colon). The number of parameters in each model (K), Akaike Information Criterion (AIC<sub>c</sub>) scores, the difference from the most parsimonious model ( $\Delta$ AIC<sub>c</sub>) and AIC<sub>c</sub> weight (wAIC<sub>c</sub>) are also shown.

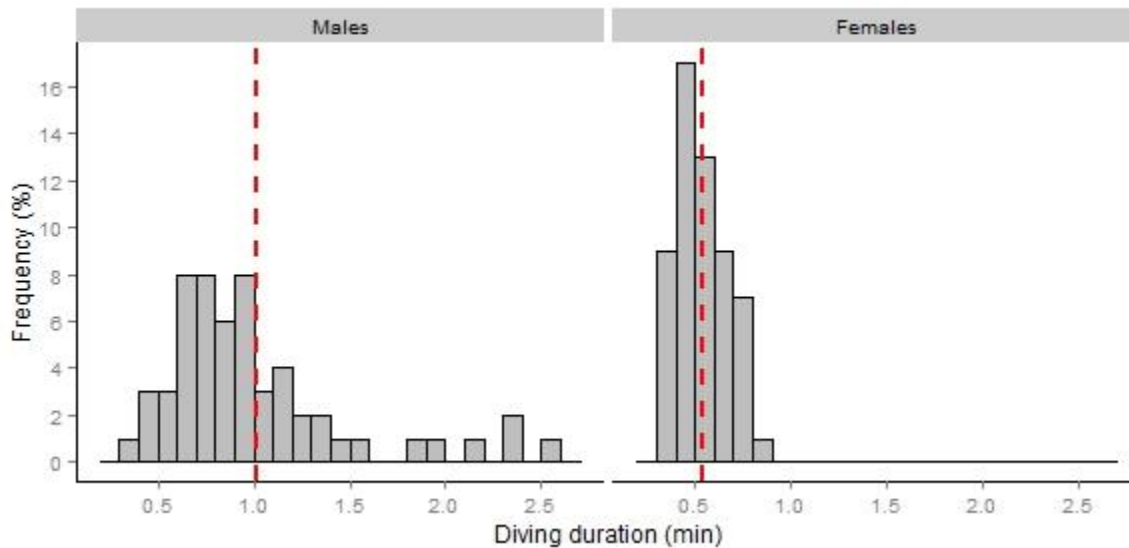
Model	Int	DC	CM	CS	Sex	DC: Sex	CM: Sex	CS: Sex	CS: CM	K	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	wAIC <sub>c</sub>
R1	•	•	•							6	582.41	0.00	0.26
R2	•	•	•		•	•				8	583.46	1.05	0.16
R3	•	•	•		•		•			8	584.01	1.60	0.12
R4	•	•	•		•					7	584.47	2.06	0.09
R5	•	•	•	•						8	584.63	2.23	0.09
R6	•	•								5	585.33	2.92	0.06
R7	•	•	•	•	•	•				10	586.80	4.39	0.03
R8	•	•	•	•	•					9	586.85	4.45	0.03
R9	•	•	•	•	•		•			10	586.86	4.45	0.03
R10	•	•		•						7	587.07	4.66	0.03
R11	•	•	•	•					•	10	587.19	4.78	0.02
R12	•	•			•					6	587.27	4.86	0.02
R13	•	•			•	•				7	587.59	5.18	0.02
R14	•	•	•	•	•			•		11	587.79	5.39	0.02
R15	•	•		•	•					8	589.19	6.78	0.01
R16	•	•	•	•	•				•	11	589.51	7.11	0.01
R17	•	•		•	•	•				9	590.25	7.84	0.01
R18	•	•		•	•			•		10	590.74	8.33	0.00
R19	•									4	601.88	19.47	0.00
R20	•				•					5	603.16	20.75	0.00
R21	•		•							5	603.38	20.97	0.00
R22	•		•		•		•			7	604.57	22.16	0.00
R23	•		•		•					6	604.73	22.32	0.00
R24	•			•						6	606.03	23.62	0.00
R25	•			•	•					7	607.54	25.13	0.00
R26	•		•	•						7	607.68	25.27	0.00
R27	•		•	•	•					8	609.26	26.85	0.00
R28	•			•	•			•		9	610.09	27.68	0.00
R29	•		•	•					•	9	610.67	28.26	0.00
R30	•		•	•	•					10	612.16	29.75	0.00

**Table S3.4.** Model selection based on AIC<sub>c</sub> explaining the individual variation in number of foraging patches visited during a foraging trip in a population of breeding European shags at Sklinna, Norway. Models were constructed using number of foraging patches (P) as a function of average distance to the colony (DC), clutch mass (CM), clutch size (CS), parental sex and parental sex interacting with distance from the colony, chick mass and clutch size and clutch mass interacting with clutch size (interactions are indicated with a colon). The number of parameters in each model (K), Akaike Information Criterion (AIC<sub>c</sub>) scores, the difference from the most parsimonious model ( $\Delta$ AIC<sub>c</sub>) and AIC<sub>c</sub> weight (wAIC<sub>c</sub>) are also shown.

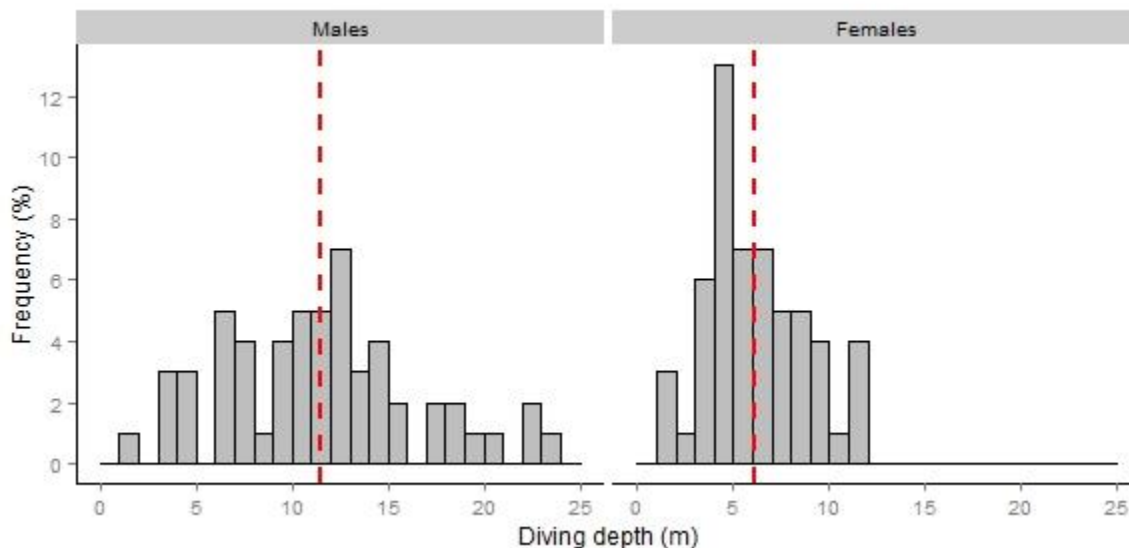
Model	Int	DC	CM	CS	Sex	DC: Sex	CM: Sex	CS: Sex	CS: CM	K	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	wAIC <sub>c</sub>
P1	•	•	•							5	315.93	0.00	0.22
P2	•		•							4	316.78	0.85	0.15
P3	•									3	317.27	1.34	0.11
P4	•	•								4	317.84	1.90	0.09
P5	•	•	•		•					6	318.09	2.16	0.08
P6	•		•		•					5	318.77	2.84	0.05
P7	•				•					4	319.23	3.29	0.04
P8	•	•	•		•	•				7	319.31	3.38	0.04
P9	•	•			•					5	319.92	3.99	0.03
P10	•	•	•	•						7	320.02	4.09	0.03
P11	•	•	•		•		•			7	320.36	4.43	0.02
P12	•	•			•	•				6	320.41	4.48	0.02
P13	•		•		•		•			6	320.97	5.04	0.02
P14	•		•	•						6	321.18	5.25	0.02
P15	•			•						5	321.49	5.56	0.01
P16	•	•		•						6	321.65	5.72	0.01
P17	•	•	•	•	•					8	322.26	6.33	0.01
P18	•		•	•	•					7	323.24	7.31	0.01
P19	•	•	•	•	•	•				9	323.40	7.47	0.01
P20	•			•	•					6	323.52	7.59	0.01
P21	•	•		•	•					7	323.82	7.89	0.00
P22	•	•		•	•	•				8	324.15	8.22	0.00
P23	•	•	•	•					•	9	324.33	8.40	0.00
P24	•	•	•	•	•		•			9	324.63	8.70	0.00
P25	•		•	•					•	8	324.94	9.01	0.00
P26	•	•	•	•	•			•		10	326.34	10.41	0.00
P27	•	•	•	•	•				•	10	326.62	10.69	0.00
P28	•		•	•	•				•	9	327.02	11.09	0.00
P29	•			•	•			•		8	327.65	11.72	0.00
P30	•	•		•	•			•		9	327.94	12.01	0.00

## APPENDIX S4: DISTRIBUTION OF DIVING DATA

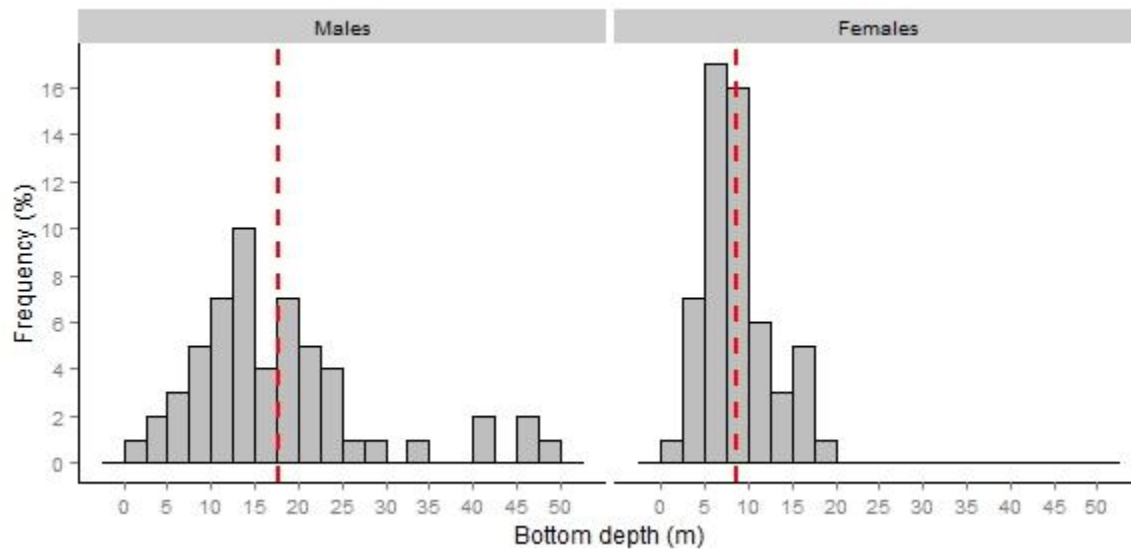
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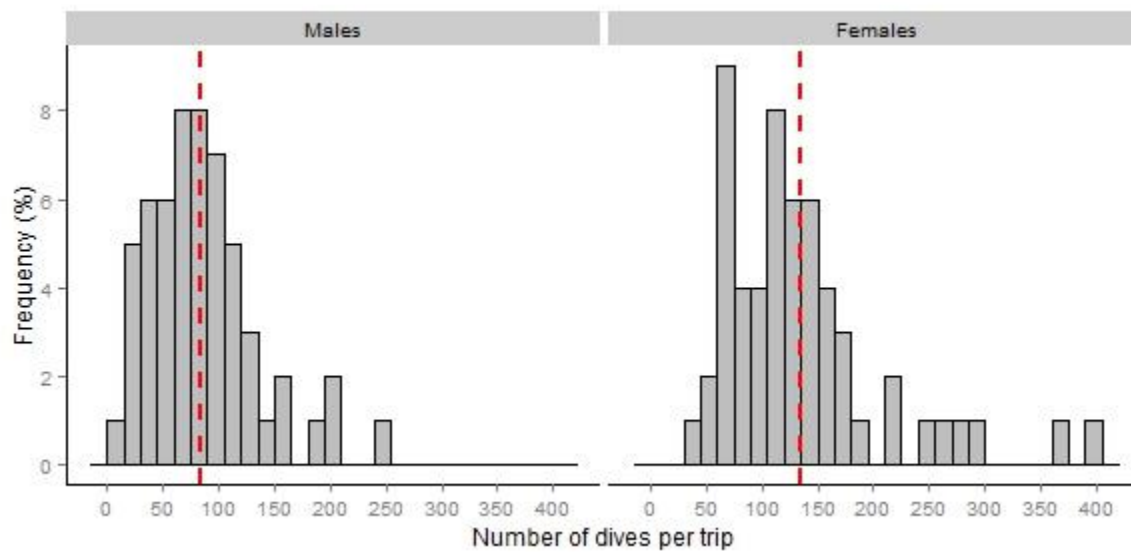
**Fig. S4.1.** The distribution of the mean diving duration (min) per dive for male and female European shags during chick rearing period at Sklinna, Norway 2013. The mean diving duration for each sex is indicated by the dashed line.



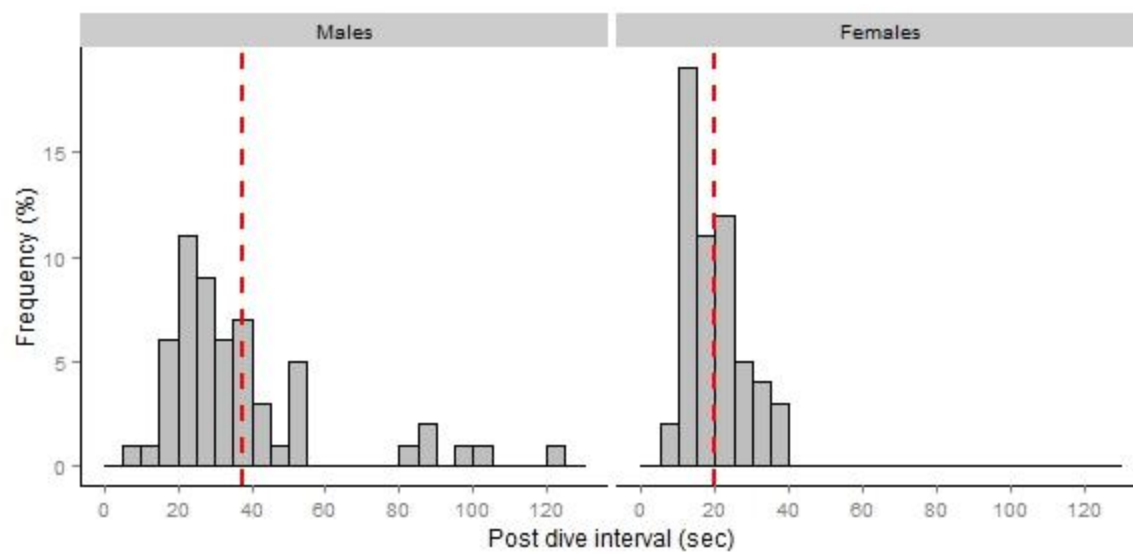
**Fig. S4.2.** The distribution of the mean diving depth (m) per dive for male and female European shags during chick rearing period at Sklinna, Norway 2013. The mean diving depth for each sex is indicated by the dashed line.



**Fig. S4.3.** The distribution of the mean bottom depth (m) per dive for male and female European shags during chick rearing period at Sklinna, Norway 2013. The mean diving depth for each sex is indicated by the dashed line.



**Fig. S4.4.** The distribution of the number of dives per foraging trip for male and female European shags during chick rearing period at Sklinna, Norway 2013. The mean diving depth for each sex is indicated by the dashed line.



**Fig. S4.5.** The distribution of the post dive interval (PDI) for male and female European shags during chick rearing period at Sklinna, Norway 2013. The mean PDI for each sex is indicated by the dashed line.