Foraging habitat and site selection do not affect feeding rates in European shags

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Summary statement: This study using acceleration-depth data loggers shows that
during chick rearing European shags did not follow classical optimal foraging rules but
instead foraged opportunistically.

Abstract

During feeding trips, central-place foragers make decisions on whether to feed at a
single site or move to other sites and/or exploit different habitats. However, for many
marine species the lack of fine resolution data on foraging behaviour and success has
hampered our ability to test whether individuals follow predictions of the optimal
foraging hypothesis. Here we tested how benthic foraging habitat usage, time spent at
feeding sites and probability of change of feeding sites affected feeding rates in

European shags *Gulosus aristotelis*, using time-depth-acceleration data loggers in 24 chick-rearing males. Foraging habitat (rocky or sandy) was identified from characteristic differences in dive patterns and body angle. Increase in body mass was estimated from changes in wing stroke frequency during flights. Bout feeding rate (increase in body mass per unit time of dive bout), did not differ between rocky and sandy habitats or in relation to the order of dive bouts during trips. Bout feeding rates did not affect the duration of flight to the next feeding site or whether the bird switched habitat. However, the likelihood of a change in habitat increased with the number of dive bouts within a trip. Our findings that shags did not actively move further or switch habitats after they fed at sites of lower quality are in contrast to the predictions of optimal foraging theory. Instead, it would appear that birds feed probabilistically in habitats of varying capture rate affected by prey density and conspecific competition or facilitation.

Introduction

Changes in feeding rate can have nutritional effects that impact an animal's energy stores and ultimately its fitness (Daunt *et al.* 2007a, Hassrick *et al.* 2013, Lescroel *et al.* 2019). Thus, knowledge of factors affecting feeding rate is essential for understanding demographic consequences of foraging behaviour. Changes in feeding rate can be considered at different temporal and spatial scales. In central-place foragers, individuals make repeated foraging trips out from a fixed point, usually the breeding colony, and on each trip they can potentially use a number of feeding sites and habitats (Monaghan et al. 1994, Boyd 1996, Sommerfeld et al. 2015). Thus, variations in feeding rate at sites may occur in relation to the habitats used and the order in which feeding sites are visited, and may also influence the decision to change site and/or habitat. At the foraging trip scale, variations in feeding rate may be related to the time spent feeding and travelling, and the number of sites and habitats used.

Foraging theory predicts that an individual is more likely to remain at a feeding site if its feeding rate is high, but move to another site in the same or a different habitat if the feeding rate is low (Stephens and Krebs 1986). Tests of these predictions have been carried out under experimental conditions (Krebs and McCleery 1984) and in semi-natural conditions (Werner and Hall 1988). However, feeding rates at multiple temporal scales have rarely been quantified in free-living animals because of the challenges of estimating the amount of food ingested, the feeding habitats used and foraging activity. Developments of a range of animal-borne data loggers for use on avian and mammalian marine predators have enabled information on habitat utilization and prey capture in free ranging individuals to be quantified using underwater images (Bowen *et al.* 2002) and accelerometry (Wilson *et al.* 2007). In avian species that mainly use flapping flight such as cormorants and auks, new techniques have also facilitated collection of data on the change in wing stroke frequency before and after foraging that provide information on changes in body mass (Sato *et al.* 2008), following the aerodynamic theory that birds adjust stroke frequency proportional to one-half the power of body mass (Rayner 1987). This technique can therefore be used to quantify food ingestion not only at whole trip scales but also at finer temporal resolution when feeding bouts are interspersed by flights.

The European shag *Gulosus aristotelis* (hereafter "shag") is a foot-propelled diver that typically feeds benthically on a wide range of fish species (Wanless and Harris 1997; Howells *et al.* 2017) and uses flapping flight to travel to and from its feeding areas. The foraging behaviour of birds in the population on the Isle of May off the coast of southeast Scotland has been studied intensively over several decades. During chick rearing, parents typically make several trips per day, each lasting several hours, to feeding areas mainly within ~10 km of the colony (Wanless and Harris 1992; Bogdanova *et al.* 2014). Data collected using VHF telemetry indicate that on a typical trip a shag makes an outward flight lasting 5 - 10 min, dives 10 - 30 times at one or more feeding sites before making a return flight back to the colony lasting 3-14 min (Wanless *et al.* 1991a, 1998).

The Isle of May is surrounded by a patchwork of sandy and rocky habitats (Wanless *et al.* 1991a). Previous work has shown that shags may feed entirely in either sandy or rocky habitat during a foraging trip or use both habitats (Watanuki *et al.* 2008).

Prey taken by this population during the chick-rearing period is predominantly lesser sandeels *Ammodytes marinus* and bottom-living fish, mainly butterfish *Pholis gunnellus*, dragonets (Callionymidae) and sculpins (Cottidae; Wanless *et al.* 1991b, Howells *et al.* 2017). Given the marked difference in habitat preference of these fish species, the assumption is that shags feeding in sandy sites are taking mainly sandeels while those feeding in rocky areas are taking butterfish, dragonets and sculpins (Wanless *et al.* 1991ab; Watanuki *et al.* 2008). The Isle of May shag population therefore, provides an ideal system in which to test predictions from foraging theory and explore relationships between feeding rates, foraging habitats, and travel times of a central-place forager.

In this study, we recorded diving behaviour, and time flying and on land using changes in depth and body acceleration and angle. We used marked differences in dive behaviour to classify dive bouts by feeding habitat (sandy or rocky). We estimated the increase in body mass during individual diving bouts ("bout food mass") and over the whole trip ("trip food mass") using changes in the wing stroke frequency during the flights before and after each dive bout and during the outbound and inbound flights at the start and end of each trip. This allowed us to estimate the bout food mass per unit time of the dive bout ("bout feeding rate") and the trip food mass per unit time "trip feeding rate").

We tested five predictions from the optimal foraging hypothesis, with three related to bout food mass or feeding rate and two related to trip food mass or feeding rate:1) Bout durations, bout food masses and bout feeding rates would be greater in sandy compared to rocky habitat since sandeels typically occur at higher densities than other benthic species (Greenstreet *et al.* 2006, Kooij *et al.,* 2008). 2) Bout food mass and bout feeding rate would be greater in later dive bouts during a trip since shags would change site if the feeding rate at the initial site was lower than average (Stephens and Krebs 1986). 3) If shags fed for longer, gained more mass and gained mass at a higher rate, they would make shorter flights or swim to the next feeding site and would not switch habitat. 4) Trip food mass would be greater when shags made longer trips and fed for longer and the trip feeding rate would be greater for parents with larger broods as they have higher energy requirements (Wanless et al. 1993). 5) Trip duration would be longer and trip food mass would be greater following longer periods of nest

attendance in order for parents to replenish their energy reserves as reported in species of Procellariiformes (Congdon et al. 2005).

Materials and methods

Fieldwork

The study was conducted on the Isle of May National Nature Reserve, south-east Scotland (56° 11'N, 02° 33'W) in the 2006 breeding season. Twenty-eight known-aged males (sexed on the basis of size and voice (Snow 1960)), brooding 1 – 3 medium-sized chicks were captured between 26 June and 2 July. Our sampling period was 2 – 4 days for each bird (Appendix 1) and ranged between 26 June and 5 July. Sampling was restricted to males to reduce variation in key foraging parameters associated with potential sex-specific differences (Daunt *et al.* 2006, Bogdanova *et al.* 2014, Lewis *et al.* 2015, Carravieri *et al.* 2020). Variation was further reduced as we sampled birds in the age range over which age effects in foraging parameters and breeding success are not apparent (3 – 17 years old) (Daunt *et al.* 1999; 2007b). Body mass was taken using a Pesola spring balance (accurate to 5 g) and a depth and acceleration data logger (D2GT, Little Leonardo Co Ltd, Tokyo; 15 mm in diameter, 53 mm in length, 18 g in mass) was attached to the back feathers with Tesa-tape. We observed behaviour after release and in all cases birds resumed brooding within 5 mins, or adopted the typical behaviour of an off-duty individual if the mate had assumed brooding duties. All individuals were recaptured at the nest 2 – 4 days later and the loggers retrieved. At recapture, body mass was measured using a Pesola spring balance. Four loggers malfunctioned or exhibited data conversion problems so our final sample size was 24 males. NatureScot granted permission to work on the island under their former name of Scottish Natural Heritage (Scientific Research Licence 6676; National Nature Reserve Permit MON/RP/69).

Data loggers were set to record surge (tail-head) (Fig. 1A) and heave (dorso-ventral) accelerations at 16Hz (Fig. 1F) and depth (at 1m accuracy) at 1Hz (Fig. 1B). Calibration of acceleration, estimation of logger attachment angle, the filter used to separate stroke-based acceleration from that caused by gravity and the protocol to estimate body angle and heave are described in Watanuki *et al.* (2005). To quantify flight duration and wing stroke cycle (1/frequency), we applied continuous wavelet transformation to take into account the non-stationary oscillation of the heave

acceleration (Fig. 1C, F, G) using Ethographer (Sakamoto *et al.* 2009). We used wavelet analyses and calculated the dominant wing stroke cycle for the window of around 7 waves (strokes) that corresponded to1 second.

To minimize the possibility of including high stroke frequency recorded during the short period of takeoff, we set the shortest wing stroke cycle as 0.16 s corresponding to the fastest wing stroke frequency of shags during cruising flight (6.250 Hz, Sato *et al*. 2008). To minimize the possibility of missing slow flapping flight but excluding very slow wing stroke during landing we set the longest wing stroke cycle as 0.20 s i.e. a little longer than the value (0.19 s) corresponding to the lowest wing stroke frequency during cruising flight (5.219 Hz, Sato *et al*. 2008). As the difference in the stroke cycles between those calculated using wo 10 (window length ~7 waves) and using wo 30 (~30 waves) was small ($\leqq 0.5\%$), we used wo 10 to optimize the accuracy and resolution of time.

To collect data over a period long enough to characterize trip and habitat of individual birds (~ 3 days), we set the sampling frequency as 16 Hz, which was lower than the sampling frequency in the previous study (64 Hz, Sato *et al*. 2008). To test the reliability of the stroke cycle in our study, we re-sampled the heave acceleration data at 16 Hz in five fly bouts of a shag collected at 64 Hz by Sato *et al*. (2008), in order to estimate the dominant cycles under two sampling regimes. We found that the difference was small ($\leqq 0.3\%$), which gave us confidence that 16 Hz sampling delivered a reliable stroke cycle.

Shags sometimes made a high frequency foot stroke (ca. 0.2 s cycles) at the start of a dive that was similar to the longest cycle of wing stroke during flight. As the duration of such high frequency foot stroke was short ($\leqq 10$ s), we defined flight (Fig. 1D) as continued high frequency stroke ($\leqq 0.2$ s cycle by definition above) longer than 10s and when birds were not diving (Fig. 1BC). We then calculated average cycle for each flight.

Dive data

Only dives deeper than 1 m were analyzed because of the accuracy of the depth sensor (± 1 m). Image data previously collected by bird-borne camera/depth loggers attached to

male Isle of May shags indicated that dives shallower than 5 m were largely associated with washing and/or surface swimming while those taken during deeper dives showed birds actively foraging near the sea floor (Watanuki *et al.* 2008). However, elsewhere shags will feed in the water column by making short (<27 s) pelagic dives (Grémillet *et al.* 1998; equivalent to ~5 m based on depth/duration relationships from our data) and this behaviour has occasionally been recorded on the Isle of May (Wanless *et al.* 1998, Carravieri *et al.* 2020). As such, we classed dives to $\leqq$5m, which constituted 13.9% of all those recorded (n=10,623), as shallow dives and retained them in the analysis.

Visual inspection of dive profiles showed that shags predominantly made U-shaped dives (Fig. 1B). Thus, different phases of a dive were readily defined from the absolute rate of change in depth (descent, > 0.6 m s^{-1}; bottom, < 0.3 m s^{-1}; ascent, $\geqq 1$ m s^{-1}, Watanuki *et al.* 2005), enabling descent duration, bottom duration, ascent duration and post dive surface duration to be estimated using the Macro Program of Igor Pro Ver. 4 (Wave Metrics). Dive duration was the sum of descent, bottom and ascent durations. As bottom depth showed very little variation within a dive, the maximum depth and mean depth recorded during the bottom phase were very similar and maximum depth was therefore defined as dive depth.

Breath-holding divers such as seabirds typically make a series of dives with short surface times followed by an extended period on the surface or in flight. Conventionally these series of dives are referred to as "dive bouts" and animals are assumed to feed in a localized site or at a single food patch during each dive bout (Feldkamp *et al.* 1989, Boyd 1996). Shag diving behaviour followed this pattern such that dives were grouped into distinct dive bouts during a foraging trip (denoted as "dive bout" in Fig. 2A, B). Dive bouts were determined using bout ending criteria as the inflection point of the log-survivorship curves, assuming that the surface time is under two random processes (movement between and within feeding sites) (Gentry and Kooyman 1986). Visual inspection of the log-survivorship curve indicated a change in slope between 200 and 300 s (Fig. S1). Accordingly we assumed dives separated by more than 250 s constituted different bouts, a broadly similar value to that found previously for this species by Grémillet *et al.* (1998). In total 522 dive bouts were identified. We assumed that dive bouts occurred within a feeding site, since surface

times between dives within a dive bout were mostly <1min (Fig. S1). Birds mainly undertook a flight before commencing a new dive bout (76%, "inter-bout flight"), but they sometimes remained on the sea after completing a bout before starting a new dive bout (24%). In the latter cases, we assumed that birds changed feeding sites by active swimming or remained in the same location in order to seek other feeding opportunities. On three occasions, shags switched habitats without undertaking a flight (dive bout20sandy to dive bout 21rocky in Fig. 2B). In 9% of dive bouts, birds made 1 – 4 flights within a dive bout ("within-bout flight e.g. fly bout30 during dive bout17rocky in Fig. 2A). The duration of each within-bout flight (0.97±0.74 min, n=57) was shorter than the duration of each inter-bout flight (3.62±3.48 min n=247) (U-test, P<0.001) so we assumed that these within- bout flights enabled birds to re-locate themselves within a feeding site when they had drifted with the water current. Among 522 dive bouts, 119 dive bouts were comprised of $\leqq$2 shallow dives ($\leqq$5m, dive bout16.1, Fig. 2A) and 23 dive bouts were comprised of $\leqq$2 deep dives ($\geqq$5m, dive bout16unknown, Fig. 2 A). These dive bouts were excluded from further analyses as we considered that they might be primarily concerned with washing, preening or exploratory behaviour.

The bout duration, number of dives, mean depth and duration of dives and bout order within the trip were calculated for each dive bout. The duration and wing stroke cycles during flights and switch of habitats (see below) between dive bouts were also recorded. Shags often made multiple flights between successive dive bouts (1 – 6 inter-bout flights), between departure from the colony and start of the first dive bout (1 – 6 outbound flights), and between the last dive bout and arrival back at the colony (1 – 5 inbound flights). Duration of inter-bout, outbound, and inbound flights was the sum of multiple flights where more than one occurred.

Trip data

To identify the period when shags were on land, we first excluded periods with dives and then used body angle data to distinguish time on land from time swimming on the surface and in flight. Shags on the sea surface or flying keep the longitudinal axis of the body almost horizontal. Time on land was therefore defined as periods of more than 60 s when the body angle was greater than 45 degrees (standing, Fig. 1A, E, Fig. 2A, B).

When shags are landing either from the air or from the water and approaching or leaving the nest, they stand and walk (Fig. 1E). However, adults brooding chicks do sometimes have a body angle <45 degrees (Fig. 2A, B). Therefore, shags were defined as being "on-land" during long dive bout intervals including standing but without flight. The frequency distribution of durations of on-land time showed three peaks with gaps around 80 min and 400 min (Fig. S2). Long periods on-land (> 1hr) typically included periods when shags had a body angle <45 degree consistent with them being at the nest brooding their chicks. Accordingly, periods on land >1hr were assumed to reflect time at the nest with the start of a trip defined as the bird standing up (body angle >45 degrees) and the end of the trip by the bird adopting an angle of body of >45 degrees. As the birds sometimes spent time on sea rocks when they came back to the island (Wanless *et al*. 1993), we also used flight after a period of standing at some other location on the island to define the end of a trip (fly bout40, Fig. 2B).

Feeding habitat

Criteria to identify bottom habitat from diving behaviour and body acceleration were developed using underwater image data from camera/depth loggers deployed on 7 male shags over the same period the accelerometry data were collected (see Watanuki *et al.* 2008 for full details on field protocols and data processing). Using data from 36 dive bouts, we carried out a discriminant analysis of dive bout characteristics to separate habitats into sandy (seabed composed of fine to coarse sand, sometimes with pebbles) and rocky (either bare rock or rock covered with kelp *Laminaria spp* or soft corals). Shags used either rocky or sandy habitats and did not switch habitat within a dive bout. Shags foraged mainly at two depths (a mode of 24 and 32 m) in sandy habitat but depths were more variable in rocky habitat (5 – 40m). Further, the proportion of dive bouts with a small coefficient of variation of dive depth (CV < 10) was greater in sandy habitat (16/16 bouts) than rocky habitat (8/20) indicating that shags changed dive depth more in rocky habitat. During the bottom phase, shags kept the angle of the body vertical in sandy habitats but horizontal in rocky ones.

Therefore, to identify bottom habitat, the dive pattern, mean bottom depth (D), coefficient of variation in the bottom depth (CV), percentage of dives where the body was horizontal during the bottom phase (pHO), percentage of dives where the bird's

head was angled downwards during the bottom phase (pDO), and trend in depth change (DT) within a bout were calculated. Body angle during the bottom phase was classed as horizontal or vertical based on the proportion of the image occupied by the seabed during the bottom phase of the dive (Watanuki *et al.* 2008). The trend in depth change was categorized using CV of bottom depth and the regression coefficient (b, $P \leqq 0.05$) of depth on dive order within a dive bout as decreasing ($b \leqq 0$, score 2), stable ($CV \leqq 10$, score 1), increasing ($b \geqq 0$, score 3) or variable ($CV \geqq 10$ and b was not significant, score 4). The discriminant function was as follows:

$$Score = 0.179*D + 0.733*CV + 1.159*pHO + 0.377*pDO + 0.064*DT$$

Using this discriminant function the analysis assigned habitat correctly in 33 out of 36 bouts (92%).

For each dive bout for the 24 male shags in the current study, we calculated the discriminant score and assigned these to rocky or sandy habitat. Postures in the bottom phase of each dive were categorized using longitudinal acceleration as "vertical" when the mode of body angle was steeper than -30° or "horizontal" when the mode of body angle was shallower than -30°. We chose -30° as a threshold because the distribution of the mode of body angle in each dive showed a weak gap around -30° (Fig. S3). Using mean bottom depth (D), CV of bottom depth, percentage number of dives with horizontal (pHO) or vertical posture (pDO) during the bottom phase and trends in change of bottom depth during the dive bout (DT), each dive bout was categorized as being in sandy or rocky habitat using this discriminant function. Habitat was identified for 379 of 380 dive bouts with $\geqq 3$ deep ($\geqq 5m$) dives. In a single dive bout with 12 deep dives, the trend of bottom depth was not determined hence habitat was not estimated.

The habitat use of the 7 male shags fitted with back-mounted cameras (20 dive bouts over rocky habitat and 16 dive bouts over sandy habitat, Watanuki *et al*. 2008) was broadly comparable to that of the 24 males in the current study (146 dive bouts over rocky and 102 dive bouts over sandy habitat, see Table 2). Ranges of mean dive depth of dive bouts over rocky (10.9—39.1 m) and sandy habitat (20.6—34.1 m) of the 7 males with cameras were comparable to median depth of dives of our 24 males (24 m

over rocky habitat and 26 m over sandy habitat, see Table 2). We were therefore confident that the 7 males with cameras could be used as reliable proxies for our study.

Food mass

We recaptured males to retrieve the loggers when they were at the nest brooding their chicks. We could not, therefore, be confident that they had not already fed the brood so we could not estimate trip food mass directly from changes in body mass to compare with values estimated from changes in wing stroke cycle.

Wing stroke cycle was calculated for flights longer than 1 min in a previous study of European shags (Sato *et al.* 2008). Here we calculated the cycle within a range of 0.16—0.20 s as in Fieldwork section for flights longer than 10 s to include as many short inter-bout flights as possible. However, the wing stroke cycle still showed increasing and decreasing trends during the short periods at the start and end, respectively, of some flights (Fig. 1C, G, Fig. 2). Durations of these takeoff and landing periods varied between flights and were difficult to define by acceleration measured at 16Hz. Then we calculated average cycle for each flight and examined variation of the average cycle across the duration of fly bouts. Variation in the average wing stroke cycle was greater for short flights but there was no trend in variation with flight duration (Fig. 3A). Shorter flights might include proportionally more time for takeoff and landing, which may cause potential errors, but not directional with the duration of flight, in body mass change estimated from wing stroke cycles. To decrease the potential for such errors for inter-bout (IB), outbound (OUT) and inbound (IN) flights where shags made multiple flights on trips, the average wing stroke cycle weighted by the duration of each flight was used (Fig. 3B). Further, we excluded outlier values (4% of fly bouts shown in Fig. 3B) where the wing stroke cycle was less or greater than the mean±2SD.

The change of body mass was estimated using the dominant wing stroke frequencies (=1/cycle) during flights before (F_1) and after (F_2) each dive bout and during the outbound and inbound flights to the nest site. Assuming that wing area, amplitude of wing stroke, and lift coefficient are constant during steady cruising flight, the stroke frequency is expected to be proportional to the square root of mass (Pennycuick 1996, Sato *et al.* 2008)

$$M_2/M_1 = (F_2/F_1)^2$$

Our aim was to estimate the increase in body mass during dive bouts and foraging trips using estimation of the proportional mass (M_2/M_1) based on the proportional wing stroke frequencies (F_2/F_1). We used the mass at capture for each individual as M_1, i.e. the "standard" mass, and estimated M_2, and, therefore, the increase in body mass during the dive bouts and trips as $M_2 - M_1$ where M_2 equals $M_1 (F_2/F_1)^2$. Variation in body mass at the start of the dive bout depends on the increase in body mass during the previous dive bout and other factors, and should be small relative to the standard mass (M_1). Similarly, variation in body mass at the start of a trip which depends on the previous time spent in the colony and other factors, should also be small relative to the standard mass (M_1). We assumed that these variations did not bias the estimate of the increase of the body mass seriously.

To estimate the increase in body mass, assumptions of constancy of wing stroke frequency with variable wind speed and that of amplitude of wing stroke with variable loads are crucial. A study using GPS tracking data for this population showed that shags flew at a relatively constant air speed (14.7 m/s on average) with little change in wing stroke frequency when the wind speeds were between -12 m/s (head wind) and + 12 m/s (tail wind) (Kogure *et al.* 2016). An experiment in cockatiels *Nyphicus hollandicus* showed that the wing stroke amplitude is not affected by loads (Hambly et al. 2004). Thus, we were confident that this technique was applicable during the relatively calm conditions in the present study.

In great cormorants *P. carbo* that have a wettable plumage (Grémillet *et al.* 2005), the increase of body mass during diving might not always represent food intake. Using the wing stroke frequency, however, Sato *et al.* (2008) estimated the body mass change in shags rearing chicks at Isle of May during each trip, and found that the mass change ranged between -30 and 260g, and the estimated body mass during the final flight back to the colony was comparable to the value directly measured on recapture. These masses were close to the mass of meals for chicks estimated by the water-offloading technique (8－208g, average 106 g, Wanless *et al.* 1993). The increases in body mass estimated for 155 sample trips (122±76 g) were similar to these previous estimates in this study. Thus, we consider that increases in body mass due to the plumage becoming wet did not seriously affect our estimation of body mass change.

We estimated the increase in body mass during a dive bout using stroke frequency before and after the dive bout (defined as bout food mass). Similarly, we estimated the increase in body mass during a foraging trip using stroke frequency during the outbound and inbound flights (defined as trip food mass).

Habitats could not be identified for >40% of the sum of dive bout durations in 8 trips and these uncategorized trips were excluded from the analyses (Appendix 1). To examine the effects of habitat and dive bout duration on the bout food mass, 248 dive bouts where both habitat and body mass change were determined were used. To test the effects of bout duration and body mass change on subsequent movement and habitat switching, those followed by land bouts were excluded. Hence sample sizes varied between tests (Table S2). Shags sometimes did not fly to the first dive bout (dive bout16unknown of Trip14, Fig. 2A) and or fly after the last dive bout (dive bout18rocky of Trip 14, Fig. 2A; 16% and 10 % of trips, respectively). Short periods on land ($\leqq$1hr) were observed shortly after leaving the nest and before dive bouts where habitats were identified (7 trips) and after the last dive bouts where habitats were identified before returning to the nest (34 trips). Similar behaviour in the Isle of May shag population was described in Wanless *et al*. (1993) using visual observations and VHF telemetry. Short periods on land were also observed between dive bouts in 29 trips (e.g. between dive bout14rocky and dive bout15rocky of Trip 13, Fig. 2A). We could not exclude the possibility that birds were at the nest during these periods on land between dive bouts. To examine the effects of trip duration, brood size, and activity budget on the body mass change and rates, 155 trips, excluding the above trips, were used.

Statistical analysis

To test effects on the frequency (number of flight or swim/rest events after a dive bout), and the values (durations of dive bout and bout mass, cumulative duration of inter-bout flights, cumulative duration of outbound and inbound flights), we used non-parametric tests (Chi-square, Wilcoxon' s signed rank test, Mann-Whitney U tests) because of small sample size. To test the relationship between mean bout feeding rate and mean trip feeding rate of individual birds, we used regression analyses where the significance of coefficient of determination was examined using ANOVA, assuming normality of these

values. For these non-parametric tests and regression analyses, we used SPSS ver 28. For GLMM, where we needed to account for repeated measures in individuals, we used library lme4 in R ver 3.2.1, (R Development Core Team 2015) and used *glmer*. We fitted all possible linear mixed models capturing all combinations of explanatory variables, with no interaction terms, and performed model selection based on Akaike Information Criteria (AIC, Burnham and Anderson 2002) using library MuMIn. Where there was a single adequate model, it was denoted as the best model and its parameter estimates and significance levels were calculated. When multiple adequate models were apparent (ΔAIC $\leqq$2.00), these were treated as equally supported models and parameter estimates and significance levels were given by full averaging. Values are shown as means and SDs in the text and tables.

Results

Dive bouts and inter-bout movements

Shags made 146 (59%) dive bouts over rocky habitat and 102 (41%) dive bouts over sandy habitat. Dive bouts over sandy habitat were significantly longer than those over rocky habitat, but median dive depth, wing stroke frequency in the flights before and after bouts, bout food mass and bout feeding rate did not differ significantly between habitats (Table 1). The best model explaining bout food mass included bout duration, bout order and habitat (Table S1A). In this analysis we did not include the number of dive bouts per trip as an explanatory variable since this was correlated with bout order (r=-0.739). Effects of bout duration and order were significant; the bout food mass was heavier for longer dive bouts (Fig. 4A) and greater in earlier dive bouts (Fig. 4B), but was independent of habitat (Table S1A). Thus, we found no support for a Prediction 1 that bout food mass would be greater in sandy habitat nor for Prediction 2 that it would be greater in later dive bouts. The latter was because bout food mass was greater in trips with a single dive bout (131.2$\pm$8.7 g, n=82) compared with bout food masses in trips with 2 dive bouts (58.3$\pm$12.5 g, n=40), 3 dive bouts (41.3$\pm$26.3 g, n=9) or more than 4 dive bouts (33.7$\pm$27.9 g, n=8). When trips with a single bout were excluded, the effect of bout order on bout food mass was not significant (Table S1C).

Three equally supported models explaining bout feeding rate were the null model and two models including order or habitat but the effect was not significant (Table S1B). Thus, we found no support for Prediction 1 that bout feeding rate would be higher in sandy habitats, nor for Prediction 2 that bout feeding rate would be higher in later dive bouts (Prediction 2). When trips with a single bout were excluded, the result was qualitatively the same (Table S1D).

Shags were more likely to fly (66% of 218 dive bouts with bout food mass) than swim/rest (34%) between dive bouts (Table S2A). The best model explaining the mode of movement (flight or swim/rest) included duration of the previous dive bouts and the effect was significant; birds tended to fly after shorter dive bouts and swim/rest after longer ones (Table S2A). The mean cumulative duration of 143 inter-bout flights was 5.1 min (range, 0.5 – 22.2 min). Cumulative duration of inter-bout flights was not related to the duration, bout food mass or bout feeding rate of the previous dive bout (Table S2B,C,D). Thus, there was only partial support for Prediction 3, with an effect of bout duration on subsequent mode of movement but not cumulative duration of flight.

Two equally supported models that explained the switch of habitat (switch or no switch) were the null model and the model including duration of the previous dive bouts but the effect was not significant (Table S2E). The bout food mass and bout feeding rate showed no clear effects on the tendency to switch habitat (Table S2F, G). Thus, there was no support for Prediction 3 that dive bout duration, bout mass gain and mass rate of gain affected the likelihood of habitat switching. Birds were more likely to fly if they switched habitat (88%, 21/24 cases) compared to if they used the same habitat (61%, 39/64 cases) ($\chi^2=5.676$ df=1 P<0.05). However, the cumulative duration of inter-bout flights did not differ when shags switched (4.6±2.6 min, n=22) or used the same habitat (3.8±2.7 min, n=38, U-test, P=0.197).

Trips

In the 155 trips where trip food mass was estimated, the mean cumulative duration of outbound flight to the first dive bout was 4.4 min (Table 2). On 80 trips there was only a single dive bout, and on the remaining 75 trips birds made 2 – 5 dive bouts (1.7 dive bouts on average). In this analysis two trips that included 6 and 7 dive bouts (Fig. 4B)

were excluded as these did not give trip food mass. The mean cumulative duration of the inbound flight from the last dive bout back to the colony was 7.4 min (Table 2). Cumulative duration of inbound flights was slightly longer than that of outbound flights for trips with a single dive bout (0.7 ± 1.6 min difference, n=80, Wilcoxon's signed rank test, P<0.001), and markedly longer for those with 2 – 5 dive bouts (5.5 ± 4.5 min difference, n=75, Wilcoxon's signed rank test, P<0.01; U-test, P<0.001) (Bonferroni-test, Fig. 5). No difference was found in the cumulative durations of inbound flight among trips with 2, 3, 4 and 5 dive bouts.

Shags used only rocky habitat on 77 trips (50%), only sandy habitat on 61 trips (39%) and both habitats on 17 trips (11%). Trips with multiple dive bouts were longer and were more likely to include both habitats (Table S3A, B), indicating that birds appeared to use rocky and sandy habitats probabilistically.

Four equally supported models explaining the trip food mass included brood size, trip duration, cumulative time of dive bout and cumulative time of inbound flight from the last dive bout (Table S1E). Based on model averaging, effects of brood size and trip duration were significant; trip food mass was greater for larger broods and after longer trips (Fig. 6A, B). The best model explaining trip feeding rate included all factors (Table S1F). However, based on model averaging, effects of brood size were marginally significant (P=0.0426) and those of other factors were not significant (Table S1F). Thus, there was support for Prediction 4 such that trip food mass was greater when shags made longer trips and fed for longer, and trip feeding rate was marginally greater for individuals with larger broods.

The duration of previous nest attendance was measured for 143 trips but was not related to the duration of the trip (r^2=0.012, NS), the bout food mass of the first dive bout (r^2=0.007, NS), or the trip food mass (r^2=0.001, NS) of the subsequent trip. Thus, we found no support for Prediction 5.

For 125 trips, bout food mass was estimated for all dive bouts. For the 78 trips where birds made only a single dive bout, trip food mass was the same, by definition, as bout food mass. For the other 47 trips where birds made 2 to 5 dive bouts, the difference between the sum of the bout food mass and the trip food mass was minor (0.9 ± 5.7 g, ranged between -9.2 g and 27.4 g).

Discussion

Although we are unable to discount the possibility that the birds may have been negatively affected by the devices, we consider that the fine-scale measurement of food intake using small, dorsally attached accelerometers causes less impact compared to other techniques such as temperature recorders in the stomach (Wilson *et al*. 1995), head-mounted recorders with magnets on the beak (Takahashi *et al*. 2004), and large dorsally attached video or still-picture camera recorders (Watanuki *et al*. 2008). Internal tags are likely to cause less impact after deployment (White *et al*. 2013, Forin-Wiart *et al*. 2018) but require surgery, so the comparison with our approach is not straightforward. A major advantage of the technique used in this study is that it estimates simultaneous foraging behaviour, thus providing fine resolution information on foraging success, flight and diving behaviour of free ranging marine predators. Using this technique with European shags we found that although feeding rates at both the bout and trip scale were highly variable, they were not related to the foraging habitat or the tendency to change feeding site.

Factors affecting bout food mass and bout feeding rate

Our results confirm that dive bout duration, i.e. time spent feeding at a site, positively affected bout food mass indicating that shags caught more prey when they dived for longer (Sato *et al*. 2008). Shags feeding in sandy habitat probe the seabed with their bills to drive out sandeels buried in the sand (Greenstreet *et al*. 2006, Kooij *et al.,* 2008). In contrast, when they are feeding in rocky habitat shags swim horizontally over the bottom searching for demersal fish among the rocks (Watanuki *et al.* 2008). Thus, we expected that bout feeding rate would be greater in sandy habitat. However, our results did not support Prediction 1 and bout feeding rate did not differ significantly between habitats. The diet of European shags varies across the breeding range and over time (Cosolo *et al*. 2011, Hillersøy and Lorentsen 2012, Howells *et al.* 2017) suggesting that shags adopt a flexible foraging strategy to exploit various prey types that are currently available. Although individual birds might differ in their use of rocky and sandy habitat, the sampling period for each bird (2 – 4 days) was short relative to the chick-rearing period (*c.*55 days, Daunt *et al.* 2007b) limiting our ability to evaluate the level of individual specialization in this population in this study. The extent to which the higher

energy density of sandeels aged > 1 year, the main age classes of sandeel that Isle of May shags prey on (4.8 to 6.5 KJ/g wet), compared to demersal fish including flatfish, butterfish, sculpin, blenny (3.3 to 5.0 KJ/g wet) (Harris and Hislop 1978, Garthe *et al*. 1996, Anthony and Roby 1996, Anthony *et al*. 2000, Takahashi *et al*. 2001; D.A.D. Grant unpublished data) relates to energy based feeding rate and individual specialization will require further work. It could also be that shags are more likely to feed with conspecifics when feeding on sandeels in sandy habitat (Watanuki *et al*. 2008). Thus, intraspecific competition may reduce feeding rates in this habitat.

In contrast to Prediction 2 that bout food mass and bout feeding rate would be greater in later dive bouts during a trip, we found that during trips where shags made more than one feeding bout, there was no support for a progressive increase in either bout food mass or bout feeding rate (Fig. 4B). We did not have independent fine-scale information on prey abundance in the study area but the data from our shags suggest that abundance might be temporally and/or spatially variable. Elsewhere cormorant species have been shown to deplete fish around the breeding colony (Birt *et al.* 1987). In our study the inbound flight was significantly longer than the outbound flight on trips with multiple dive bouts. This pattern indicates that shags moved progressively further away from the colony on successive dive bouts as would be predicted by the Storer-Ashmole 'halo' hypothesis (Storer 1952; Ashmole 1963). Alternatively, individuals might remember sites with high density and/or abundance of prey near the colony and visit these first. In accordance with this, birds fed more during dive bouts in trips with a single dive bout than those with multiple dive bouts. Little penguins *Eudyptula minor* made trips repeatedly to the same sites when feeding success was high (Carroll *et al.* 2018). However, we did not have location data to allow us to test this possibility. The pattern we observed might also be explained by shags visiting sites probabilistically and spending longer at the first feeding site in order to fulfil their own energy requirements before starting to catch food to bring back to the brood. However, the lack of relationship between the duration of the previous period in the colony and the bout food mass of the first dive bout of the subsequent trip (Prediction 5) does not support this explanation.

Prediction 3 was that if shags fed for longer, gained more mass and gained mass at a higher rate, they would make shorter flights or swim to the next feeding site and

would not switch habitat. We found partial support for this prediction such that shags tended to fly rather than swim or rest after shorter dive bouts indicating that they moved further, but flight duration after shorter dive bouts did not differ significantly compared to longer bouts. Bout feeding rate also did not affect the flight time to the next dive bout. Although shags tended to fly when they switched habitat, they did not show a propensity to switch habitat after shorter dive bouts when they gained less mass. Bout feeding rate also did not affect the switch in habitat. Thus, our findings indicated that shags did not actively move further and/or switch habitats after they fed at sites of lower quality where density and/or abundance of prey was lower. This provides further support for shags visiting sites probabilistically. Other factors potentially include unpredictability of prey at a fine temporal scale. Shags do not have discrete feeding territories; instead they share their foraging environment with conspecifics and other avian, mammalian and fish predators. Particularly in sandy habitat shags feed communally (Watanuki *et al.* 2008) and conspecific interference competition and/or facilitation may affect prey availability. Thus, it could be that optimal foraging rules break down under these conditions or at least are much weaker. However, collecting data on predator interactions under field conditions, in order to test this assertion, would be very challenging.

Factors affecting trip food mass and trip feeding rate

In accordance with Prediction 4, we found a positive effect of brood size and trip duration on trip food mass (Fig. 6). Wanless *et al.* (1993) found that the mass of stomach contents at the end of a trip was positively correlated with the total mass of chicks of each brood. These results indicate that adults adjust trip food mass according to the food requirements of their chicks. However, the effect of brood size on trip feeding rate was marginal (Table S1F). This indicates that individuals with larger broods increase the food brought back to the colony mainly by increasing the trip duration rather than increasing feeding rate.

The duration of the previous nest attendance did not relate to the subsequent trip duration and trip food mass, so Prediction 5 was not supported. A previous study on the Isle of May noted that shags often spent time on the sea rocks at the end of a trip and speculated that they were digesting prey for their own requirements before returning to

the nest to feed the brood (Wanless *et al.* 1993). Interestingly, we found that in trips with multiple dive bouts, the sum of bout food masses was almost identical to the trip food mass. This indicates that chick-rearing shags do not digest food during inter-dive bout time during trips. Rather, they retain all the food in the stomach until they return to the colony and then either allocate it for their own energy requirements or use it to provision the brood. In *Pygoscelid* penguins parents possibly feed and digest food for themselves in the early part of trips and store food in their stomach for chicks thereafter by regulating digestion processes (Peters 1997). However, foraging trips of penguins are substantially longer than those of shags (~24 hours compared to ~2 hours) which may enable shags to retain all the food caught during a trip without the need for this regulatory process. Species of Procellariiformes that typically feed much further away from the colony than European shags, regulate the allocation of food for chicks and for themselves by alternating long and short trips (Weimerskirch *et al*. 1984) whereby long trips are used to feed and digest food for replenishing their energy reserves following long nest attendance (Congdon *et al*. 2005). Our results therefore indicate that inshore feeding and offshore feeding species may adopt different energy allocation strategies.

In conclusion, male European shags on the Isle of May did not follow classical optimal foraging rules and specifically did not regulate foraging according to the feeding rate in the previous feeding site. As such, it would appear that they feed probabilistically in habitats of varying capture rate affected by prey density and conspecific competition or facilitation. This strategy, whereby average rates of feeding were similar in the two main habitats used, enabled shags to largely achieve their primary objective to sustain energy requirements for themselves and their brood.

Competing interests

No competing interests declared

Data availability

Dryad Data Depository http//datadryd.org

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Figures and Tables
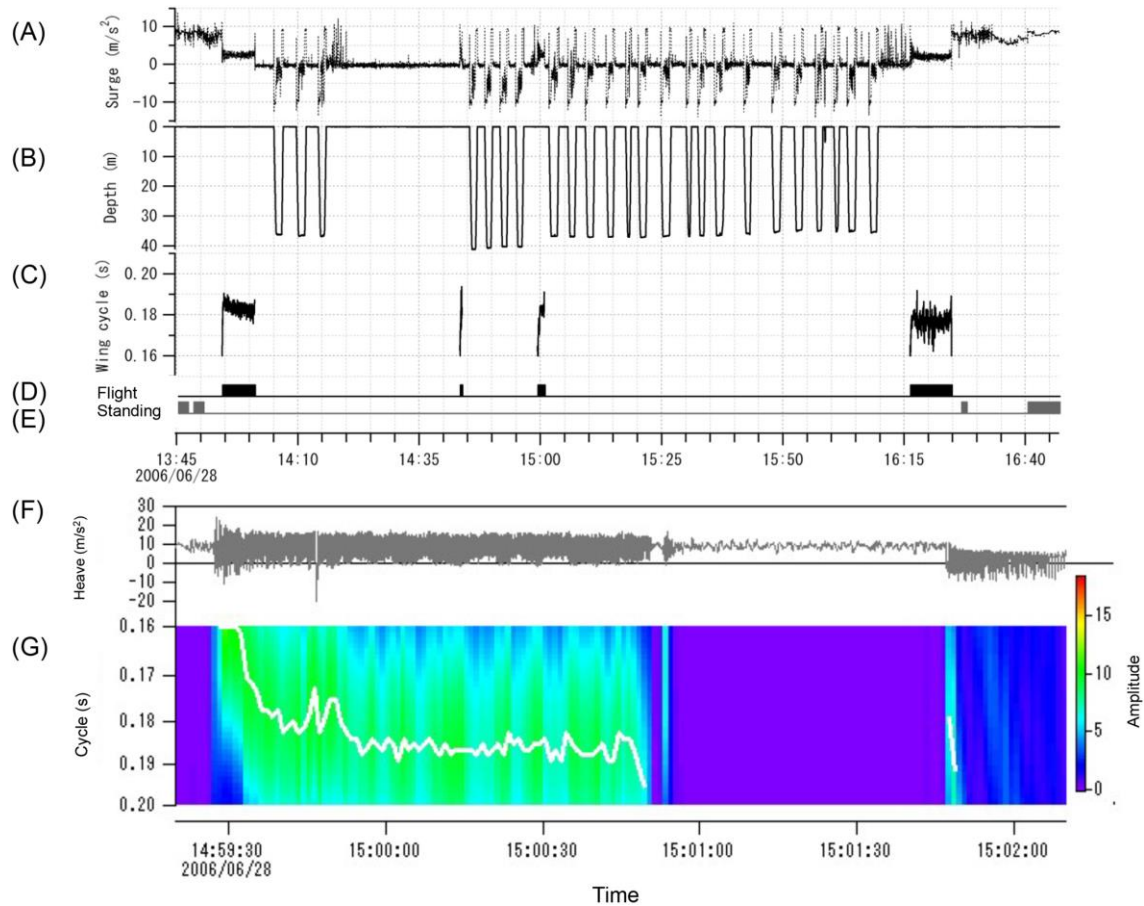
Fig. 1. Body acceleration and diving. Body acceleration, dive depth, wing stroke cycle and behaviour (flight or standing) during a foraging trip (A-E) and body acceleration during a flight (enlarged) between 14:59:20 and 15:02:10 (F). (A) 16 Hz surge (tail-head) acceleration reflecting body angle and wing stroke, (B) diving behaviour showing a dive bout, (C) wing stroke cycle calculated by continuous wavelet transformation of heave (dorso-ventral) acceleration, and periods of (D) flight and (E) standing determined by wing stroke and body angle, respectively. (F) Low-pass filtered heave acceleration and (G) its amplitude across the wing stroke cycles calculated by continuous wavelet transformation of heave acceleration. The change of the dominant cycle is shown by gross white line in (G). Wing stroke cycle was short (0.17 - 0.16 s) at the start of flying (14:59:30 in (G)) and subsequently became longer (0.19 - 0.18 s). Note that the stroke cycle (0.19 – 0.18 s) produced by foot propulsion was also observed at the start of diving around 15:01:45 in (G).
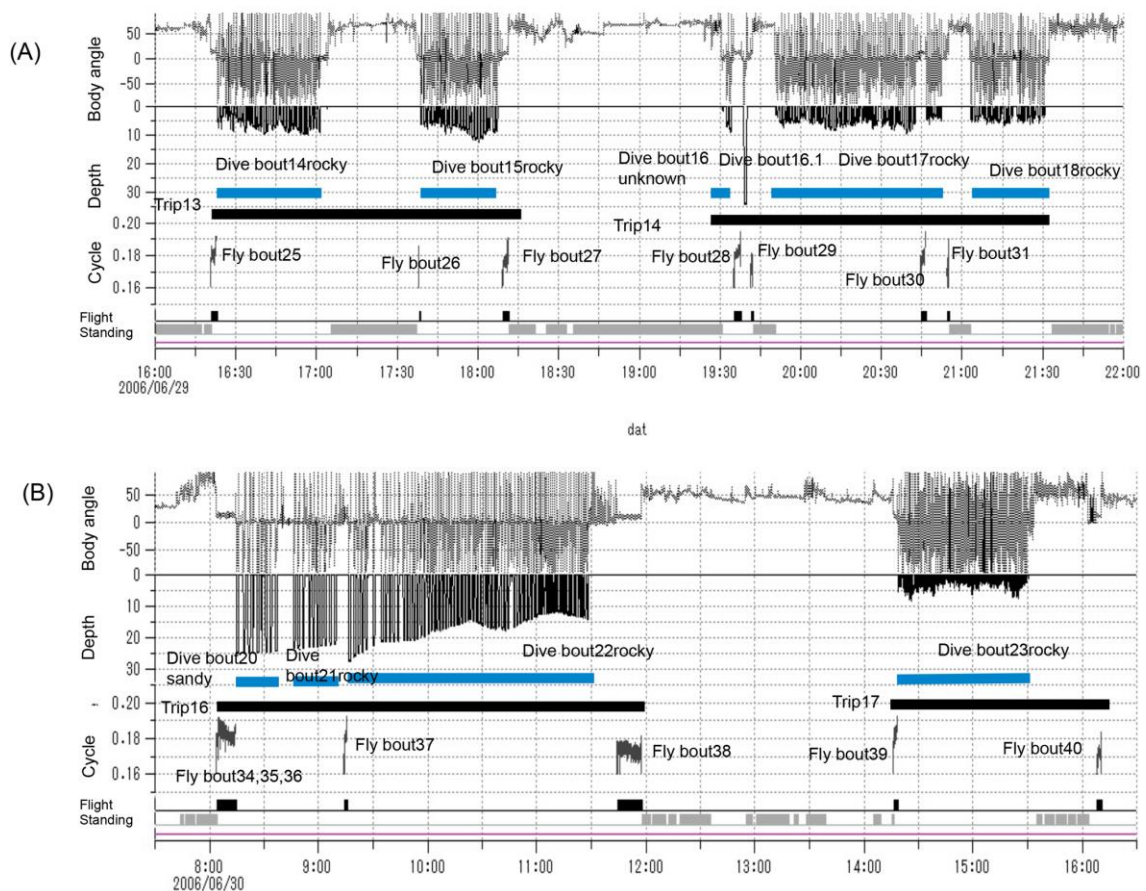
Fig. 2. Two examples of foraging trips. Trips (black horizontal line), dive bout (blue horizontal line), and the change of the cycle of fly bouts are shown. Habitats of dive bouts were rocky, sandy and unknown. Body angle (degrees), depth (m) and the cycle (s) of wing stroke during flight, periods of flight and when birds were standing are shown. (A) Bird 361JUL1 left the nest, flew (fly bout 25), dived (dive bout 14 over rocky habitat), swam to the land, remained ashore for around 45 min including time standing for 30 min, then flew (fly bout 26) and dived (dive bout 15 over rocky habitat), then flew back (fly bout 27) to the nest (Trip 13). We could not exclude the possibility that this bird visited its nest during a short ($\leqq$1hr) period on land between dive bouts 14 and 15. The bird left its nest again and swam and undertook a dive bout 16 (habitat unknown), flew (fly bout 28) and made a single deep dive (as dive bout 16.1), flew (fly bout 29) to the land, then swam and made long dive bout 17 over rocky habitat that included a within-bout flight (fly bout 30), then flew (fly bout 31) to the land, then swam and carried out a dive bout 18 over rocky habitat and swam back to the nest (Trip

14). Observational data would suggest that these short on-land periods (times between bouts 16 and 17, and between dive bouts 17 and 18) were those when the bird was on sea rocks not at the nest. (B) The following morning the same bird (361JUL1), made a series of flights (fly bouts 34~36), undertook a dive bout 20 over sandy habitat, swam and carried out a dive bout 21 over rocky habitat, flew (fly bout 37) and made a long dive bout 22 over rocky habitat, then flew (fly bout 38) back to the nest (Trip 16). The stroke frequency of the outbound flight at the start of Trip 16 was the weighted average of the cycles of fly bouts 34~36. The bird left the nest again and flew (fly bout 39) and made a dive bout 23 over rocky habitat, swam to land, stand on rock for a while then flew (fly bout 40) back to the nest (Trip 17).
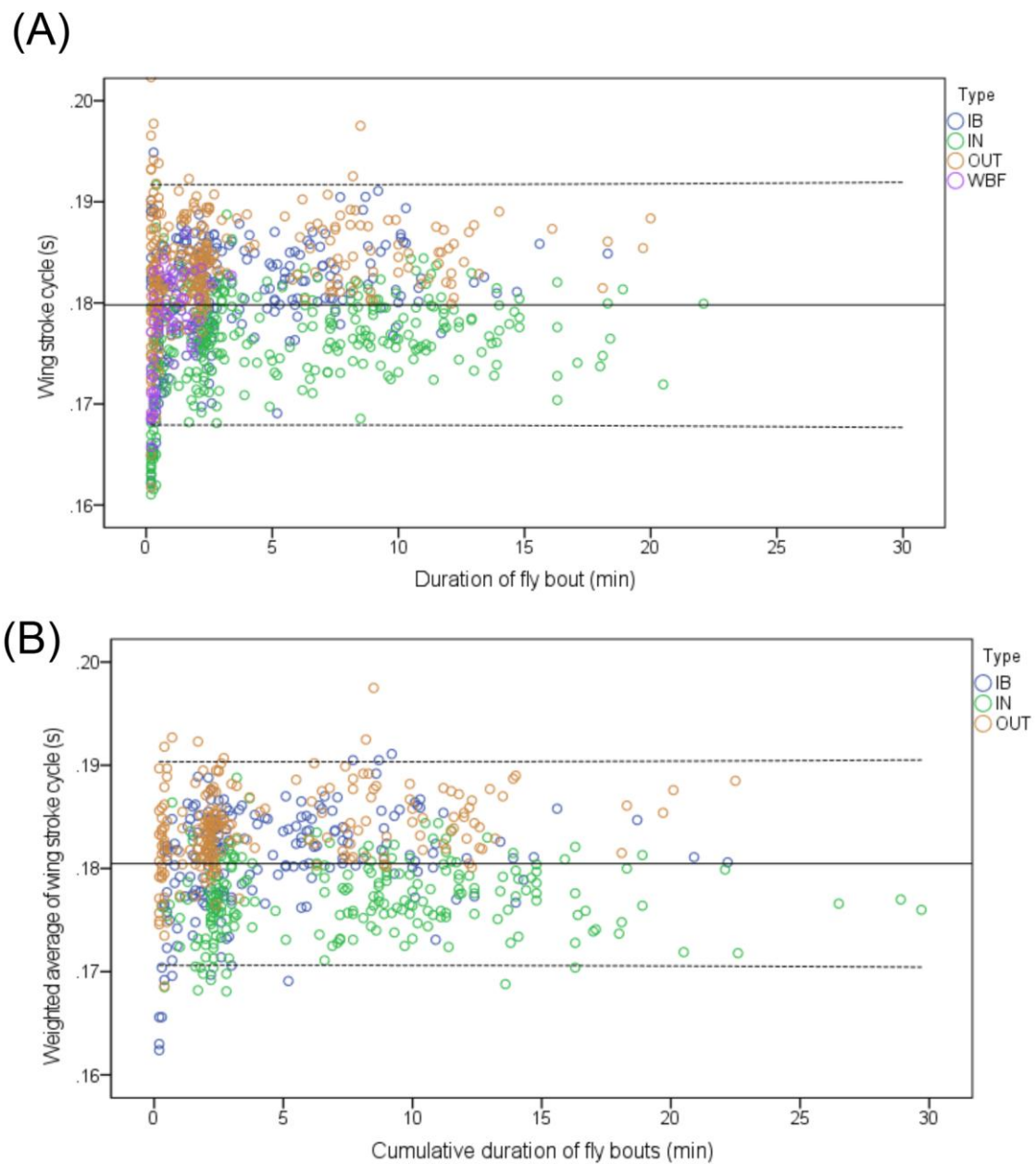
Fig. 3. Duration of flights and calculated wing stroke cycle (A) Wing stroke cycle during each flight (> 10s) calculated using the power spectral density across the range of 0.16-0.20 s vs duration of each of outbound (OUT), inbound (IN), inter-bout (IB) and within dive bout (WBF) flights. (B) Weighted average of wing stroke cycle vs the cumulative duration of outbound (OUT), inbound (IN) and inter-bout (IB) flights. Mean and 95% confidence ranges are shown by lines and dotted lines, respectively.
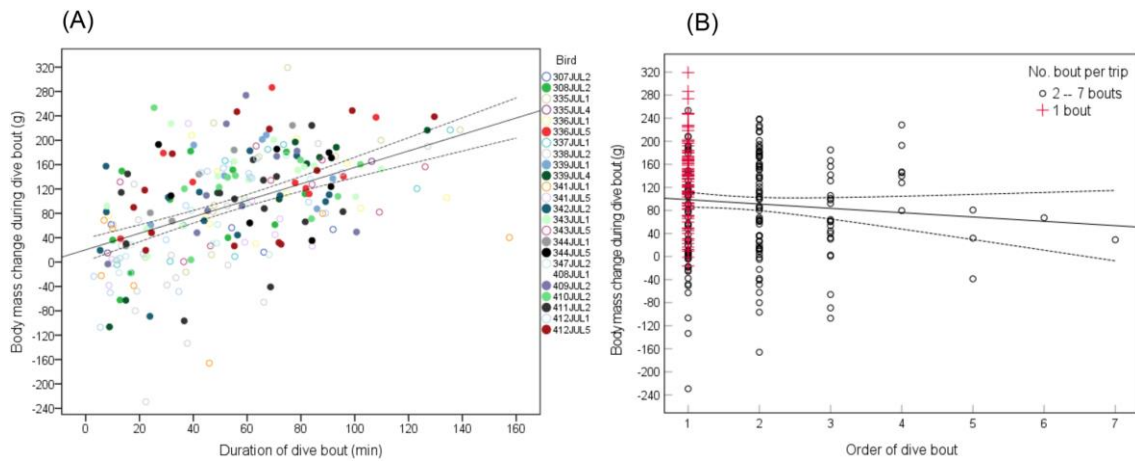
Fig. 4. Increase in body mass during a dive bout. Effects of (A) duration of dive bout and (B) order of dive bout within a trip on the increase in body mass during dive bouts (bout food mass) where habitats were identified (n=248 dive bouts). Symbols are individual birds for (A) and the number of dive bouts per trip for trips with only a single dive bout and those with 2 to 7 dive bouts for (B). Linear regression line (solid line) with 95% confidence intervals (broken line) is shown.
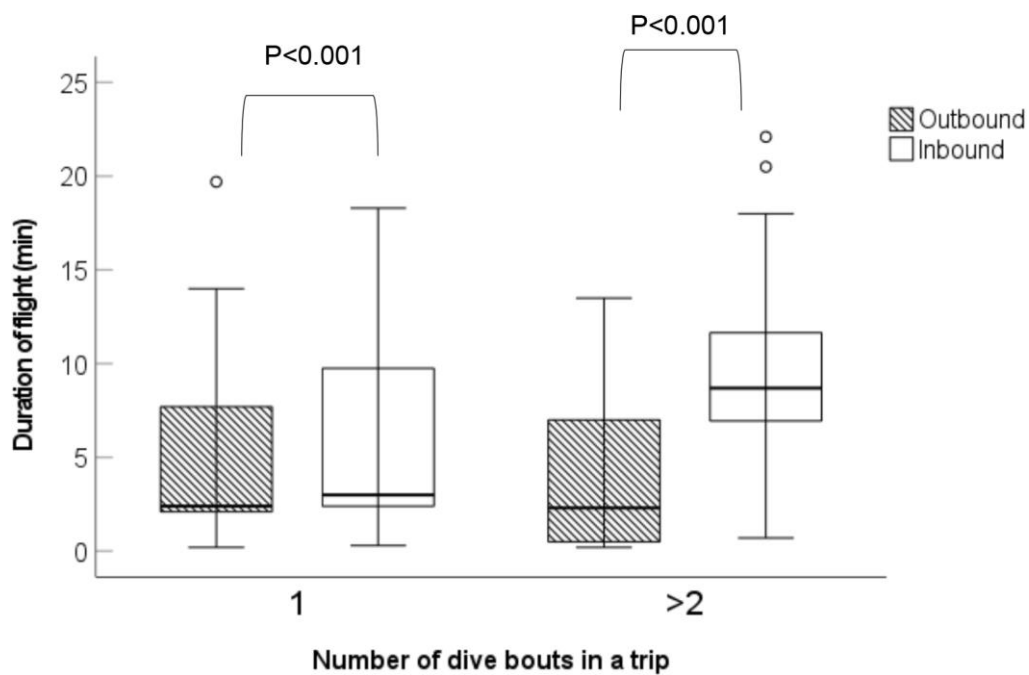
Fig. 5. Outbound and inbound flights. Duration of the outbound flight to the first dive bout and inbound flight from the last dive bout for trips with a single dive bout and those with 2 to 5 dive bouts. As we excluded those when trip food masses were not calculated in the analyses of trip, so maximum number of bouts was 5 hear. Boxes indicate median and 1st and 3rd quartiles. Whiskers indicate minimum and maximum values, excluding outliers shown by circles (values >1.5 × interquartile range). Significance of the differences between the durations of inbound and outbound flights are shown.
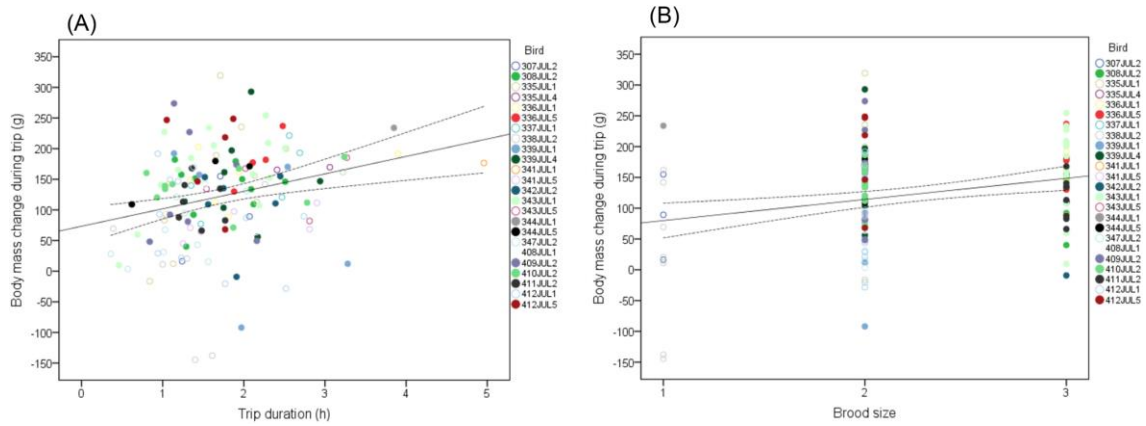
Fig. 6. Increase in body mass during trip. Effects of (A) trip duration and (B) brood size on the increase in body mass (trip food mass) during trips (n=155 trips). The same symbols (individual birds) are used as in Fig. 4. Linear regression line (solid line) with 95% confidence intervals (broken lines) is shown.

Table 1. Duration of dive bouts, wing stroke frequnecy (n/s) in the flights before and after bouts, bout food mass (total amoun of food taken during dive bout) , bout feeding rate (bout food mass per unit time of dive bout) and median dive depth during dive bouts over rocky (n=146 dive bouts) and sandy habitats (n=102 dive bouts). Mean±SD, range in parenthesis and results of U-test are shown.

	Rocky habitat	Sandy habitat	P
Duration of dive bouts (min)	51±32 (3 -- 139)	56±30 (5 -- 157)	0.018
Wing stroke frequency before bout	5.47±0.11(5.25 -- 5.80)	5.46±0.10 (5.26 -- 5.78)	0.323
Wing stroke frequency after bout	5.60±0.14 (5.33 -- 5.87)	5.60±0.12 (5.30 -- 5/86)	0.982
Bout food mass (g)	91±89 (-229 -- 253)	97±84 (-166 -- 319)	0.958
Bout feeding rate (g/min)	1.7±3.6 (-20 -- 11)	2.0±2.9 (-4.9 -- 21)	0.363
Median dive depth (m)	24±10 (3 -- 49)	26±8 (5 -- 41)	0.057

Table 2. Mean ± SD, meaidan and range of trip duration, cumulative duration of outbound and inbound flights, the number of dive bouts,   the number of inter-bout flights betwen dive bouts, the proportion of time for the   sum of dive bout, the proportion of time   for the sum of inbound and outbound flights, the proportion of time for the sum of inter-bout flight time between dive bouts, the proportion of time on land near the start and end of trips, and the trip food mass (mass of food in the stomach at the end of trip) and the trip feeding rate(trip food mass per unit time of trip) in 155 trips.   Note that the maximum number of dive bouts per trip was reduced to be five in these 155 trip samples.

	Mean±SD	Median	Range
Trip duration (h)	1.72±0.72	1.61	0.36 -- 4.96
Cumulative duration of outbound flight (min)	4.4±4.2	2.4	0.1 -- 19.7
Cumulative duration of inbound flight (min)	7.4±4.9	7.5	0.3 -- 28.9
No. of dive bouts per trip	1.7±0.9	1	1 -- 5
No. fly bouts between dive bouts per trip	0.6±1.0	0	0 -- 7
%Time dive bout	72±13	73	23 -- 94
%Time for outbound and inbound flights	12±7	10	1 -- 37
%Time flight between bouts	2±3	0	0 -- 15
%Time on land	4±9	0	0 -- 38
Trip food mass (g)	122±77	135	-144 -- 319
Trip feeding rate (g/h)	77±54	75	-104 -- 241

Appendix 1. Bird ID (logger ID and date of recapture, "JUL2" means 2 of July), period of deployment (day and hour), age (years), brood size, body mass (g), the number of dives, median dive depth (m), median dive duration (s), median bottom time (s) with ranges in parenthesis. The number of trips with known habitats, untyped trips where habitats of >40% of dive bouts were unknown, the number of trips including land time between dive bout hence excluded from the analyses, the number of trips giving the value of the change of body mass (stomach content mass, g), the number of feeding bout on rocky, sandy and unknown habitats during the trips of individual birds.

Bird ID	Period	Age	Brood	Mass	Dives	Depth	Duration	Bottom	Trip	Untyped	With land	With meal	Rocky	Sandy	Unknown
307JUL2	3d18h	10	1	2030	363	30(1-35)	73(1-120)	38(0-80)	10	0	1	3	8	5	11
308JUL2	3d16h	8	3	1920	197	35(1-41)	97(1-136)	49(0-98)	11	1	0	10	16	1	8
335JUL1	3d13h	10	2	2040	428	28(1-40)	72(2-110)	36(0-63)	14	0	1	12	12	8	3
335JUL4	3d	5	2	1810	156	27(1-30)	76(1-109)	42(0-72)	4	0	0	2	8	0	6
336JUL1	3d4h	15	3	1790	1540	4(1-34)	26(1-90)	16(0-64)	14	2	2	8	18	1	5
336JUL5	3d4h	4	3	1960	515	25(1-34)	72(1-109)	39(0-65)	11	0	1	4	9	8	7
337JUL1	3d16h	8	2	1890	586	6(1-50)	39(1-135)	27(0-82)	7	2	2	5	8	7	14
338JUL2	3d18h	5	1	1890	324	34(1-48)	78(1-137)	35(0-77)	12	0	1	7	22	1	5
339JUL1	3d2h	4	2	2060	590	14(1-83)	53(2-86)	32(0-69)	11	0	1	5	17	0	7
339JUL4	3d2h	5	2	1940	409	24(1-38)	56(1-110)	26(0-69)	8	0	0	7	10	0	7
341JUL1	3d16h	6	2	1800	476	8(1-43)	33(1-87)	21(0-52)	7	1	2	1	3	14	10
341JUL5	2d10h	3	2	1750	440	15(1-38)	58(1-105)	33(0-58)	8	0	2	7	6	9	5
342JUL2	3d16h	11	3	1790	596	11(1-35)	42(2-74)	26(0-47)	11	0	4	9	1	16	9
343JUL1	3d17h	9	3	1950	473	22(1-47)	66(2-103)	37(0-61)	14	0	0	14	9	8	2
343JUL5	3d19h	12	2	1830	410	31(1-49)	73(1-128)	36(0-80)	10	0	1	5	5	8	4
344JUL1	3d15h	8	1	1850	377	25(1-38)	59(1-104)	26(0-58)	7	0	2	3	14	5	9
344JUL5	3d13h	4	2	1710	367	31(1-37)	75(2-99)	39(0-58)	9	0	1	3	4	8	4
347JUL2	3d15h	10	2	1870	213	34(1-51)	89(1-134)	47(0-87)	12	0	0	11	7	12	2
408JUL1	2d22h	16	2	1870	246	30(1-35)	74(1-109)	40(0-66)	9	0	0	9	2	10	1
409JUL2	3d15h	8	2	1840	258	31(1-40)	83(2-126)	46(0-79)	10	1	0	7	4	8	6

410JUL2	3d19h	9	2	2010	336	29(1-35)	71(1-109)	37(0-60)	10	0	0	9	4	7	3
411JUL2	3d14h	9	3	1910	414	30(1-37)	76(1-109)	41(0-65)	13	0	5	11	9	10	0
412JUL1	3d15h	3	2	1825	441	23(1-48)	61(2-147)	31(0-86)	12	1	1	12	19	0	9
412JUL5	3d14h	3	2	1730	468	31(1-33)	72(2-95)	36(0-55)	10	0	2	7	9	9	6
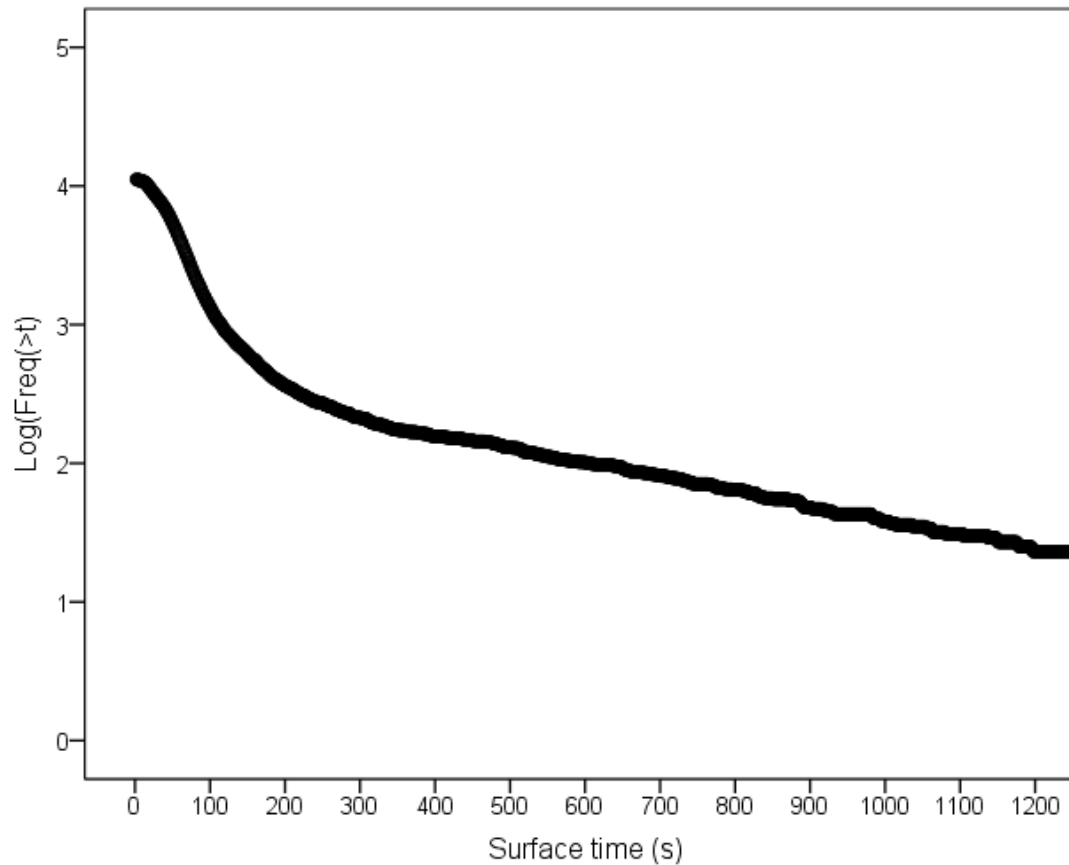
Fig. S1. Dive bouts were determined using bout ending criteria as the inflection point of the log-survivorship curves for surface interval between dives. Bout ending criteria was assumed to be 250s.
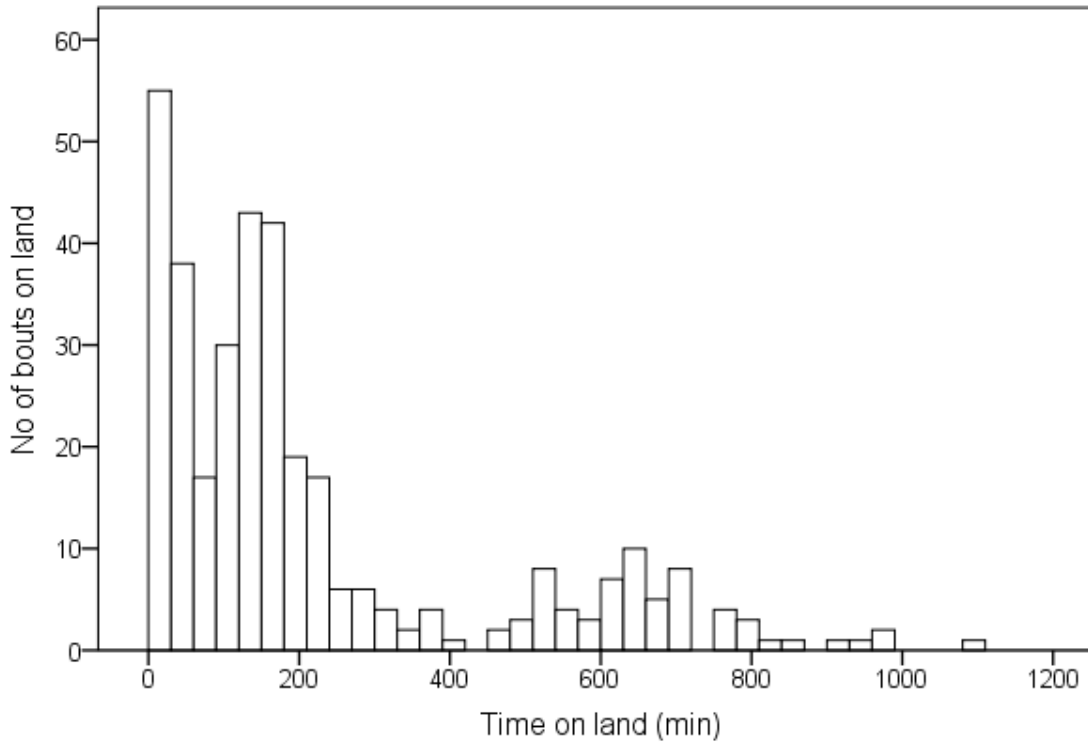
Fig. S2. Distribution of the duration of time on land. Time between dive bouts that was longer than 60 min and including standing (the body angle was greater than 45 degrees) was defined as time on land. The gaps are observed around 80 min and 400 min. Long (≧1hr) on land time was for attending chicks. Those longer than 7 hr was for attending chicks over nights and those shorter than 1 hr might be for resting on the rock during the trips. In this study birds were defined to start the trips when they left the nests by walking (standing) and to finish the trips when they arrived at the nests by walking (standing), then spent long time (≧1hr) on land possibly attending the chicks.
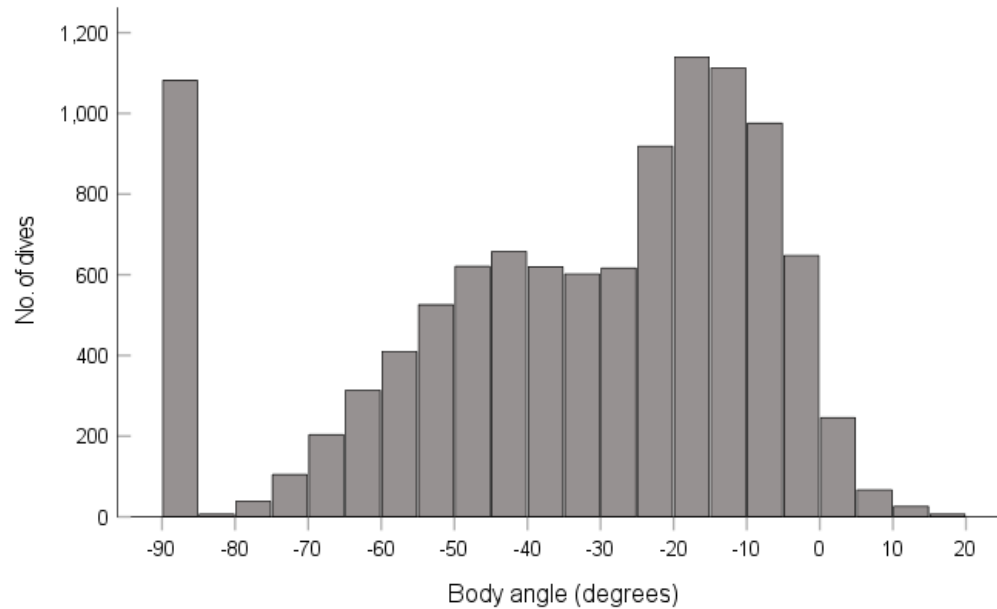
Fig. S3. Distribution of the mode of body angle during the bottom phase for 10,959 dives with the bottom phase. Dives without bottom phase (n=1,134) were excluded. As frontal images taken by camera-loggers showed that body angle during the bottom phase was close to vertical in sandy habitats but horizontal in rocky ones (Watanuki et al. 2008), postures, categorized using longitudinal acceleration as "vertical" when they had mode of body angle steeper than -30° or "horizontal" when mode of body angle was shallower than -30°. Body angles of dives with angle <-90 degree, possibly because of measurement error, was assumed to be -90 degree (Watanuki et al. 2005). So, frequency of dives with -90 degree was extraordinary high.

Table S1. Model selection and parameter estimates for feeding during dive bout and during trip.

Model selection (basing on Δ AIC) for factors affecting A) bout food mass and B) bout feeding rate during dive bout using all bouts (248 dive bouts). Effects were examined using LMM (lme in R). Bird identity was a randon factor. Candidates of explanatory factors were duration of dive bout (BD), habitat (Hab; sandy vs rocky), and the order of bout within each trip (Ord). The same analyses were carried out using the dive bouts only in the trips with multiple number of dive bouts (166 dive bouts) for C) bout food mass and D) bout feeding rate. Also similar model selection was performed for factors affecting E) trip food mass and F) trip feeding rate. Sample was 155 trips. Candidates of explanatory factors were brood size (BR), cumulative duration of inbound flight from the last dive bout (InF), cumulative time of dive bouts (TB), and trip duration (TD), or proportional time of the sum of the time for dive bouts (pTB), that of the sum of flight (pTF) and that of time on land (pTL) per trip. Models, degree of freedam, Akaike Information Criteria (AIC), ΔAIC, and Akaike weight are shown. The best model or equally supported models (ΔAIC<2.00) are in bold. Parameter estimates ±standard errors and t or z values for the best models and full average are shown for the bout food mass and bout feeding rate, respectively.

A) Bout food mass (n=248 dive bouts)

Model selection

Model	df	logLik	AIC	ΔAIC	weight
BD+Hab+Ord	**6**	**-1409.16**	**2830.3**	**0**	**0.951**
BD+Ord	5	-1413.465	2836.9	6.61	0.035
BD+Hab	5	-1414.462	2838.9	8.6	0.013
BD	4	-1418.34	2844.7	14.36	0.001
Hab+Ord	5	-1442.353	2894.7	64.39	0
Hab	4	-1445.408	2898.8	68.49	0
Ord	4	-1445.774	2899.5	69.23	0
NULL	3	-1448.815	2903.6	73.31	0

Parameter estimates for the best model

	Estimate	Std. Error	df	t-value	P
(Intercept)	47.9312	13.4917	157.26	3.553	0.000504
Duration of dive bout	1.3319	0.1499	240.8	8.886	<0.001
Habitat(sandy)	-15.2363	10.5925	196.57	-1.438	0.15191
Order	-11.8184	4.9892	243.7	-2.369	0.018626

B) Bout feeding rate (n=248 dive bouts)

Model selection

Model	df	logLik	AIC	ΔAIC	weight
NULL	**3**	**-651.787**	**1309.6**	**0**	**0.457**
Ord	**4**	**-651.41**	**1310.8**	**1.25**	**0.245**
Hab	**4**	**-651.649**	**1311.3**	**1.72**	**0.193**
Hab+Ord	5	-651.261	1312.5	2.95	0.105

Parameter estimates by model averaging (full average)

	Estimate	Std. Error	Adjusted SE	z-value	P
(Intercept)	1.169347	1.132802	1.133231	1.032	0.302
Order	-0.10841	0.197999	0.198437	0.546	0.585
Habitat(Sandy)	-0.001441	0.251526	0.252772	0.006	0.995

C) Bout food mass for dive bouts in trips with multiple dive bouts (n=166 dive bouts)

Model selection

Model	df	logLik	AIC	ΔAIC	weight
BD+Hab+Ord	**6**	**-946.044**	**1904.1**	**0**	**0.832**
BD+Hab	5	-949.133	1908.3	4.18	0.103
BD+Ord	5	-949.72	1909.4	5.35	0.057
BD	4	-952.791	1913.6	9.49	0.007
Hab+Ord	5	-968.444	1946.9	42.8	0
Hab	4	-972.028	1952.1	47.97	0
Ord	4	-972.127	1952.3	48.17	0
NULL	3	-975.715	1957.4	53.34	0

Parameter estimates for the best model

	Estimate	Std. Error	df	t-value	P
(Intercept)	25.1315	15.2576	136.11	1.647	0.102
Duration of dive bout	1.3397	0.1831	158.93	7.318	<0.001
Habitat(sandy)	-7.6335	13.5209	128.38	-0.565	0.573
Order	-5.2103	6.0461	161.45	-0.862	0.39

Table S1 (contnued)

D) Bout feeding rate for dive bouts in trips with multiple dive bouts (n=166 dive bouts)

Model selection

Model	df	logLik	AIC	ΔAIC	weight
NULL	3	-464.583	935.2	0	0.407
Hab	4	-463.854	935.7	0.54	0.31
Ord	4	-464.512	937	1.86	0.161
Hab+Ord	5	-463.791	937.6	2.42	0.122

Parameter estimates by model averaging (full average)

	Estimate	Std. Error	Adjusted SE	z-value	P
(Intercept)	1.08696	1.03234	1.03382	1.051	0.293
Habitat(Sandy)	0.18552	0.50305	0.50617	0.367	0.714
Order	-0.07125	0.19563	0.19661	0.362	0.717

E) Trip food mass (n=155 trips)

Model selection

Model	df	logLik	AIC	ΔAIC	weight
BR+InF+TD	6	-868.779	1749.6	0	0.343
BR+TD	5	-870.077	1750.2	0.6	0.255
BR+InF+TB+TD	7	-868.111	1750.2	0.66	0.246
BR+TB+TD	6	-869.622	1751.2	1.69	0.148
InF+TD	5	-874.773	1759.5	9.99	0.002
TD	4	-876.252	1760.5	10.95	0.001
InF+TB	6	-874.282	1760.6	11.01	0.001
BR+InF+TB	6	-874.527	1761.1	11.5	0.001
TB+TD	5	-875.688	1761.4	11.82	0.001
BR+TB	5	-876.094	1762.2	12.63	0.001
BR+InF	5	-876.214	1762.4	12.87	0.001
BR	4	-878.762	1765.5	15.97	0
InF+TB	5	-879.96	1769.9	20.36	0
InF	4	-881.031	1770.1	20.51	0
TB	4	-882.187	1772.4	22.82	0
NUL	3	-884.363	1774.7	25.17	0

Parameter estimates by model averaging (full average)

	Estimate	Std. Error	Adjusted SE	z-value	p
(Intercept)	4.75	33.3673	33.6318	0.141	0.8877
Brood size	32.1958	13.1635	13.2671	2.427	0.0152
Inbound fly	-0.267	1.2132	1.2223	0.218	0.8271
Trip duration	35.2771	17.5442	17.6463	1.999	0.0456
Time of dive bout	-0.1722	0.3531	0.3549	0.485	0.6275

F) Trip feeding rate (n=155 trips)

Model selection

Model	df	logLik	AIC	ΔAIC	weight
BR+pTB+pTF+pTL	7	-813.738	1641.5	0	0.937
BR+pTF+pTL	6	-818.625	1649.2	7.77	0.019
BR+pTB+pTF	6	-818.84	1649.7	8.2	0.016
pTB+pTF+pTL	6	-818.888	1649.8	8.3	0.015
BR+pTB	6	-819.119	1650.2	8.76	0.012
BR+pTF	5	-823.485	1657	15.49	0
BR+pTL	5	-823.619	1657.2	15.76	0
pTF+pTL	5	-823.866	1657.7	16.26	0
BR+pBT	5	-824.002	1658	16.53	0
pTB+pTF	5	-824.038	1658.1	16.6	0
pTB+pTL	5	-824.642	1659.3	17.81	0
BR	4	-828.439	1664.9	23.4	0
pTF	4	-828.727	1665.5	23.98	0
pTL	4	-829.169	1666.3	24.86	0
pTB	4	-829.511	1667	25.55	0
NUL	3	-833.979	1674	32.48	0

Parameter estimates for the best model

Best model	Estimate	Std. Error	df	t-value	P
(Intercept)	15.68	47.53	125.9	0.33	0.742
Brood size	19.176	8.748	16.96	2.192	0.0426
pTFly	33.727	80.011	129.52	0.422	0.6741
pTBout	18.01	49.573	142.04	0.363	0.7169
pTLand	24.045	60.691	149.72	0.396	0.6925

Table S2. Model selection and parameter estimates for movement between diving bouts

Model selection (basing on Δ AIC) for testing A) effects of the duration of the dive bouts on the mode of movement (fly or swim) to the following dive bouts and B) those on the cumulative duration of inter-bout flight to the following dive bouts, and C) effects of the bout food mass and D) those of the bout feeding rate on the cululative duration of inter-bout flight to the following dive bouts. Also similar model selection was performed for testing effects of E) duration of dive bouts, F) bout food mass and G) bout feeding rate on the switch of habitat to the following dive bouts. Effects were examined using GLMM (lme in R) with binomial function (A, E, F, G) or using LMM (lme in R) (B, C, D). Bird identity was a randon factor. Candidates of explanatory factor were the duration of dive bout (BD) (A, B, E), bout food mass (MIB) (C, F), and bout feeding rate (Frate) (D, G). Models, degree of freedam, Akaike Information Criteria (AIC), ΔAIC, and Akaike weight are shown. The best or equaly suported models (ΔAIC<2.00) are in bold. To test the effects of duration, body mass change or feeding rate of dive bouts on the following movement and habitat switch, those followed by on land time was excluded. Parameter estimates ±standard errors and t-values for the best models and z-values for the full average models are shown. Effects of bout food mass on the mode of movement can't be tested as bout food mass was not estimated

A)Mode of movement (218 dive bout)

Model selection

Models	df	logLik	AIC	ΔAIC	weight
BD	3	-133.984	274	0	0.974
NULL	2	-138.623	281.2	7.28	0.026

Parameter estimate for the best model

	Estimate	Std. Error	z-value	P
(Intercept)	1.118632	0.244997	4.566	4.97E-06
Duration of dive bout	-0.018497	0.006214	-2.977	0.00292

B)Cumulative duration of inter-bout flight to the following dive bouts (143 dive bouts)

Model selection

Model	df	logLik	AIC	ΔAIC	weight
NULL	3	-393.654	793.3	0	0.552
BD	4	-392.862	793.7	0.41	0.448

Parameter estimate for average model (full average)

	Estimate	Std. Error	Adjusted SE	z-value	P
(Intercept)	2.57854	2.87695	2.87725	0.896	0.37
Duration of dive bout	-0.0192	0.02342	0.02345	0.819	0.413

C)Cumulative duration of inter-bout flight from the dive bouts with bout food mass data (94 dive bouts)

Model selection

Model	df	logLik	AIC	ΔAIC	weight
NULL	3	-255.878	517.8	0	0.976
MIB	4	-258.6	525.2	7.44	0.024

D)Cumulative duration of inter-bout flight from the dive bouts with bout feeding rate data (94 dive bouts)

Model selection

Model	df	logLik	AIC	ΔAIC	weight
NULL	3	-255.878	517.8	0	0.976
Frate	4	-261.726	531.5	13.69	0.001

E)Switch of habitat to the following dive bouts (88 dive bouts)

Model selection

Model	df	logLik	AIC	ΔAIC	weight
NULL	2	-50.731	105.5	0	0.73
BD	3	-50.723	107.4	1.98	0.27

Parameter estimate for average model (full average)

	Estimate	Std. Error	Adjusted SE	z-value	P
(Intercept)	-0.2768476	0.514323	0.5159549	0.537	0.592
Duration of dive bout	-0.0004227	0.0065861	0.0066801	0.063	0.95

Table S2 (continued)

F)Switch of habitat from the dive bouts with mass data (49 dive bouts)

Model selection

Models	df	logLik	AIC	ΔAIC	weight
MIB	3	-26.837	59.7	0	0.516
NULL	2	-27.899	59.8	0.12	0.484

Parameter estimate for average model (full average)

	Estimate	Std. Error	Adjusted SE	z-value	P
(Intercept)	-0.638913	0.789182	0.797437	0.801	0.423
Bout food mass	0.00453	0.006453	0.006548	0.692	0.489

G)Switch of habitat from the dive bouts with mass data (49 dive bouts)

Model selection

Models	df	logLik	AIC	ΔAIC	weight
NULL	2	-27.899	59.8	0	0.66
FRate	3	-27.58	61.16	1.36	0.34

Parameter estimate for average model (full average)

	Estimate	Std. Error	Adjusted SE	z-value	p
(Intercept)	-0.36392	0.6416	0.64799	0.562	0.574
Bout feeding rate	0.03528	0.09419	0.09604	0.367	0.713

Table S3. Model selection and parameter estimates for the number of bouts and trip duration

Model selection (basing on Δ AIC) for factors affecting A) trip duration where candidates of explanatory factors were the brood size (BR) and the number of dive bouts (nB) and B) the number of habitats (1 or 2) used in each trip where candidate of factors were the number of dive bouts of known habitats (nKB). Parameter estimates ±standard errors and t-values for the best model are shown. Effects were examined using LMM (lmer in R). Bird identity was a randon factor. Models, degree of freedam, Akaike Information Criteria (AIC), ΔAIC, and Akaike weight are shown. The best models (ΔAIC<2.00) are in bold.

A) Trip duration (n=155 trips)

Model selection

Model	df	logLik	AIC	ΔAIC	weight
nB	4	-149.37	306.7	0	0.865
BR+nB	5	-150.227	310.5	3.72	0.135
NULL	3	-168.529	343.1	36.32	0
BR	4	-169.333	346.7	39.93	0

Parameter estimates for the best model

	Estimate	Std. Error	df	t-value	P
(Intercept)	1.1077	0.12948	44.04	8.555	6.48E-11
Number of bout	0.40465	0.05824	152.66	6.948	1.01E-10

B) The number of habitats per trip (n=155 trips)

Model selection

Model	df	logLik	AIC	ΔAIC	weight
nKB	4	-21.268	50.5	0	1
NULL	3	-42.22	90.4	39.9	0

Parameter estimates for the best model

	Estimate	Std. Error	df	t-value	P
(Intercept)	0.7383	0.05723	101	12.9	< 2e-16
No of bouts with known habitat	0.26392	0.03573	152.99	7.387	9.06E-12