



FEATURE ARTICLE

# Luck and tactics in foraging success: the case of the imperial shag

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**ABSTRACT:** It has been proposed that predators searching for prey acquire food according to a probabilistic framework, where success is based on 'luck' and the odds of success vary with prey abundance. If true, this has major ramifications for variation in the rates of energy acquisition within animal populations, which is particularly pertinent in offspring provisioning and breeding success, because smaller animals (the young) cannot starve for as long as the adults. However, despite much general speculation about rates of food acquisition, no study has measured whether food encounter is probabilistic in wild animals. We used animal-mounted cameras to document all prey captures by wild imperial shags *Leucocarbo atriceps* as they hunted underwater and show that, although they mostly do not have inter-prey acquisition time distributions that accord with a 'luck-based' framework assuming a constant probability of finding prey over time, there is no difference in the predicted amount of food captured between models that use the empirical data or theoretical Poisson-based fits of the data. We also noted considerable inter-individual differences in foraging success that far exceeded any differences between empirical and theoretical inter-prey acquisition time distributions. The data were used in a probabilistic foraging model that made explicit the mechanistic link between random prey encounters and food-dependent breeding success, indicating that 'less lucky' individuals could not provision their broods at rates commensurate with normal growth while the 'lucky' birds could do so easily. Given the nature of food encounter in these birds, coupled with substantial inter-individual variation in foraging success, we suggest that more successful individuals are particularly choosy about when, how



Imperial shag are extraordinary birds that catch prey at depths of tens of metres underwater. The challenge is to determine how they do this.

Photo: Andrea Benvenuti

and where to forage, which results in them operating with higher odds of success.

**KEY WORDS:** *Leucocarbo atriceps* · Cormorant · Foraging ecology · Gambling · Probability of food encounter · Tactics

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## 1. INTRODUCTION

The acquisition of food, essential for all animals, is under strong selection pressure to be efficient because high rates of energy acquisition underpin rapid transfer of resources to progeny, which improves lifetime reproductive success (Côté et al. 2004). In sit-and-wait predators such as flatfish (Nilsson et al. 2010), it has been assumed that prey acquisition depends on luck (McNamara & Houston 1990). However, even the seemingly more refined option where predators move through the environment to increase the rate of food encounter (Weimerskirch et al. 2007) has been suggested to be luck-based, with the chances of prey encounter couched in terms of probabilities (Wilson et al. 2018) which presumably change over time and space. This is very different from many energy acquisition models that assume that energy gain can be well-described by simple mean rates of food acquisition (e.g. dos Santos & Jobling 1995). However, when such assumptions are extrapolated to breeding animals, studies may ignore the variability in the rate at which food can be delivered to offspring, and this variability can affect lifetime reproductive output (van Daalen & Caswell 2017). Specifically, rarefaction in food availability can have a disproportionate effect in magnifying inter-individual variability in the luck-based scenario, which is predicted to affect offspring provisioning and thereby breeding success (Wilson et al. 2018). Critically though, to our knowledge, no study has tested the extent to which food acquisition by wild animals operating freely across time and space can be usefully represented by Poisson modelling and how this affects the predicted consequences for breeding success.

In this work, we quantified food encounters by using miniature video recorders on wild imperial shags *Leucocarbo atriceps* to observe them foraging underwater as they feed to provision themselves and their brood. We used these birds because, at our study site, they have a particularly easy-to-model diet, consisting principally of a combination of 'small' (ca. 2 g) and 'large' (ca. 20 g) prey (Gonzalez Miri & Malacalza 1999). Thus, variation in the rate of energy acquisition depends simply on the rates of prey encounter and the distribution of the encountered prey between the 2 size classes and their respective calorific values. We applied the information that we gained on food-finding events to examine how well the data fit with a Poisson model of prey encounter in which a constant rate of probability of prey capture is assumed. We also examined how predicted variation in cumulative food-finding across time in breeding birds

compares between Poisson and empirical models. We then developed an approach to examine the consequences of the observed variation in individual foraging success in their predicted breeding success, manifest by the amounts of food delivered to the brood across time consisting of multiple foraging trips.

## 2. MATERIALS AND METHODS

### 2.1. Field work

Fieldwork was conducted during November 2015 and 2016 at Punta León, Chubut, Argentina (43° 04' S, 64° 29' W). Cameras (61 mm long, 21 mm wide, 15 mm tall, 29 g, 1280 × 960 pixels, 30 frames s<sup>-1</sup>; Little Leonardo), which filmed the interaction between birds and their prey (Gómez-Laich et al. 2015), were deployed during the first days of the chick-rearing period on 11 female imperial shags. The total weight of the device was less than 1.4 % of the average adult female body mass (Svagelj & Quintana 2007). We did not document the length of foraging trips of a control group of unequipped birds, so device effects as judged by this metric could not be evaluated. Only females were used because they are the primary provisioners for the brood (Giudici 2018). All cameras were programmed to record in continuous mode and to start recording in the morning on the day after instrumentation, since female imperial shags depart the colony after sunrise and return at midday (Harris et al. 2013). Devices were attached to the upper back of the animals with Tesa tape following Wilson et al. (1997) and were left on for a single foraging trip and recovered when the birds returned to their nests to provision their chicks. In order to minimize the potential detrimental effects of attached devices, we did not use any position-determining systems, such as GPS, in tandem. Subsequently, video data were observed carefully using the free video player Kinovea ([www.kinovea.org/](http://www.kinovea.org/)) to determine the timings of prey captures (to the nearest second) and the size and type of prey ingested. The lengths of time between all prey ingestions, which seemed readily visible, were collated for each individual bird.

### 2.2. Modelling probabilistic foraging success in resource gathering

We modelled the provision of food for the brood by modelling the energy reserves of a foraging individual (Fig. S1 in the Supplement at [www.int-res.com/](http://www.int-res.com/)

articles/suppl/m682p001\_supp.pdf). In this model, we divide time into foraging and non-foraging periods. During non-foraging periods, energy reserves decline at a constant rate dependent on the metabolic rate of the birds at the colony (see Section 2.3). Periods of foraging activity were modelled using a random process to calculate the net energy accumulated (cf. Stephens & Charnov 1982). There are 2 separate aspects to the randomness in this model:

(1) the times at which prey is encountered and captured are assumed to be random across the foraging period; and

(2) the size of the energy gain from the prey captured is assumed to be random.

For the first aspect we use a ‘renewal counting process’,  $N_t$ , which counts the number of captured prey items up to time  $t$ . Let  $S_t$  denote the random time at which the  $(j-1)^{\text{th}}$  encounter and successful capture occurred (the ‘success time’). The time elapsed between the  $(j-1)^{\text{th}}$  and  $j^{\text{th}}$  capture is denoted by  $T_j$  (the ‘inter-occurrence time’) so that  $S_j = S_{j-1} + T_j$  and  $N_t = n$  if and only if  $S_n \leq t \leq S_{n+1}$ . In a renewal counting process, it is assumed that these inter-occurrence times  $T_j$  are independent and share a common distribution (Rolski et al. 1999). Here, for simplicity, we assume that there is (effectively) no handling time required (cf. Dawes & Souza 2013) and that prey are encountered and captured without loss.

For the second aspect, we assume that at the  $j^{\text{th}}$  success, the forager gains a random amount of energy  $X_j$ , determined by the size of the prey captured. We assume that all  $X_j$  are independent and share some common distribution.

Combining these 2 aspects together, if we denote the energy reserves of the foraging animal at time  $t$  by  $E_t$  and the cost of foraging per unit time as  $c$ , which we assume to be constant, we then have:

$$E_t = E_0 - ct + \sum_{j=1}^{N_t} X_j \quad (1)$$

during periods of time when the animal is foraging. Eq. (1) is our renewal model for the energy reserves for a foraging animal (this energy reserves process  $E_t$  is an example of a ‘storage process’; Prabhu 1998).

In this study, the distribution of the prey size is particularly simple, as there are only 2 possible prey sizes, which we denote as small (with an energy gain of  $g$ ) and large (with an energy gain of  $G$ ). Thus, the distribution of  $X_j$  is determined by  $P(X_j = g) = P(\text{small}) = p$  and  $P(X_j = G) = P(\text{large}) = q$  where  $P$  denotes probability and  $p + q = 1$ . It follows that the mean and variance of the energy gain for each success are given by:

$$E(X_j) = \mu = gp + Gq \quad (2)$$

$$\text{Var}(X_j) = pq(G - g)^2 \quad (3)$$

where  $E$  denotes the mean ( $\mu$ ) and  $\text{Var}$  the variance. To simplify the model, we also assume that, as time elapses, the forager randomly encounters and captures prey items with a constant probability of success per unit time  $P_s$  (which assumes that there is no appreciable patchiness [cf. Arditi & Dacorogna 1988] in the foraging area, which is likely to be an oversimplification). Under this key assumption, the counting process  $N_t$  is known as a ‘Poisson process’ and the total energy gain  $\sum_{j=1}^{N_t}$  as a ‘compound Poisson process’. It can be shown that  $N_t$  follows a Poisson distribution with parameter  $P_s t$ , and each inter-occurrence time  $T_j$  follows an exponential distribution with parameter  $1/P_s$ .

We then have:

$$E(N_t) = P_s t, \quad (4)$$

$$\text{Var}(N_t) = P_s t, \quad (5)$$

$$E(T_j) = \frac{1}{P_s}, \quad (6)$$

$$\text{Var}(T_j) = \frac{1}{P_s^2} \quad (7)$$

and:

$$E(E_t) = E_0 - ct + \mu P_s t \quad (8)$$

$$\text{Var}(E_t) = P_s t (g^2 p + G^2 q) \quad (9)$$

We refer to this model of energy accumulation as our ‘Poisson model’ for foraging. The parameters  $c$ ,  $g$  and  $G$ , as well as the length of foraging and non-foraging periods, are determined in Section 2.3 and are viewed as fixed across individuals. The parameters  $p$  and  $P_s$  were determined for each individual from data collected in the fieldwork (see Section 2.3). This Poisson model can be thought of as a generalisation of the model presented previously by Wilson et al. (2018), with the model adapted by making time continuous and introducing randomness to size of the prey captured (Fig. 1).

To assess how accurately the assumption of constant probability of success is reflected in the ‘inter-occurrence time’ data, we performed Lillefors-corrected Kolmogorov-Smirnov tests using the function ‘LcKS’ in the ‘KScorrect’ package (R Core Team

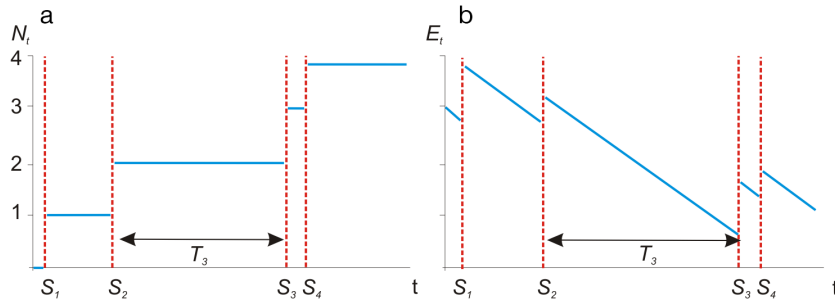


Fig. 1. Example (a) counting process ( $N_i$ : number of prey items) and (b) corresponding energy reserves process ( $E_i$ : energetic state) indicating the success times ( $S$  with subscript) and an inter-occurrence time ( $T$ ). The blue lines in (a) highlight the cumulative number of prey items taken over time, while those in (b) illustrate the state of energy of the bird, increasing on prey ingestion and decreasing during the search for the next prey item

2019), both on each individual and also on the combined data from all individuals which had been normalized (so that each individual has a mean of 1, which effectively provided a scaling so that all individuals had a  $P_s = 1$ ) to test if they were exponentially distributed.

### 2.3. Simulating the effects of observed probabilistic foraging success on breeding success

Since the female imperial shag is the primary provider of food to the chicks (Giudici 2018), we assumed that the males had no input in provisioning, although we note that similar work can be readily modified for other species to incorporate both parents provisioning.

It was assumed that all birds had a maximum amount of time to forage, which was set to 7 h (mean  $\pm$  SD =  $5.8 \pm 1.2$  h; Gómez-Laich et al. 2012) because imperial shags from this colony do not forage at night (Harris et al. 2013) and both parents have to forage once per day during daylight. The foraging cost was calculated assuming that birds expend 40% of the foraging time diving and 60% of their foraging time floating (Gómez Laich et al. 2012). Using the equation presented by Gómez Laich et al. (2011) and considering a diving overall dynamic body acceleration (ODBA) of  $0.39 g$  (Gómez-Laich et al. 2013) and a floating ODBA of  $0.08 g$  (Gómez Laich et al. 2011), we estimated a diving cost of  $28.2 \text{ W kg}^{-1}$  and a floating cost of  $15.4 \text{ W kg}^{-1}$ . Multiplying these values by 1.9 kg (the mean weight of female imperial shags; Svagelj & Quintana 2007) and considering the proportion of time engaged in each of the 2 activities gives us a foraging cost of 38.9 W. The non-foraging costs were calculated using a flying cost of  $95.4 \text{ W kg}^{-1}$  (Pennycuik 2008) for 6% of their non-foraging time

(Gómez Laich et al. 2012) and a resting cost, calculated for a similar cormorant species (European shag *Gulosus aristotelis*) of  $9.4 \text{ W kg}^{-1}$  (Enstipp et al. 2006), for 94% of their non-foraging time (Gómez Laich et al. 2012), multiplied by 1.9 kg to obtain a non-foraging power of 27.7 W. The overall cost of not foraging was calculated by multiplying the energetic cost of not foraging by the amount of time birds spent not foraging (17 h) and gave us a value of  $1685.4 \text{ kJ d}^{-1}$ .

Video information of dives where shags were foraging along the seafloor

allowed us to detect capture attempts and searching behaviour. Capture attempts were classified into 2 broad categories: those that lasted between 2 and 5 s and those that lasted  $\geq 5$  s. Short capture attempts were always associated with the ingestion of *Ribeiroclinus eigenmanni* ('small prey') while the longest capture attempts were associated with the consumption of *Raneya gluminensis* ('large prey'). These are the 2 principal fish species consumed by Punta León imperial shags during the early chick-rearing period (Gonzalez Miri & Malacalza 1999). Differences in the proportion of small and large prey caught between individuals were analysed by means of a chi-squared test of homogeneity of proportions using the 'chisq.test' function in the 'stats' package (R Core Team 2019).

For each bird, the time elapsed between each capture attempt was computed and was employed to calculate the rate of probability of success via Eq. (6) using the sample mean for each individual. The weight and energetic value of both prey species ( $23.9 \text{ g}$  and  $4351 \text{ J g}^{-1}$  for *R. fluminensis* and  $2.3 \text{ g}$  and  $4100 \text{ J g}^{-1}$  for *R. eigenmanni*) were obtained from Gonzalez Miri & Malacalza (1999). Assuming an assimilation efficiency of 0.8 (Enstipp et al. 2006), the energy gain of the 'large' and 'small' prey was taken to be 83 191 and 7544 J, respectively.

We assumed that, initially, all adults began foraging with body energy levels given by  $E_{\text{ideal}} - E_{\text{non-forage}}$ , where  $E_{\text{ideal}}$  is the ideal/standard body state and  $E_{\text{non-forage}}$  is the energy spent not foraging for a single period between the last time the bird fed and the time it went to sea. Prey were acquired probabilistically according to the model outlined above with the energy reserves calculated according to the model.

During foraging, the birds were considered to attempt to accrue their own energetic costs so that they arrived back at the nest at an energetic state of  $E_{\text{ideal}}$  plus an amount to be allocated to their brood of 2



chicks, which varied with age. The masses of food given to a 2-chick brood as a function of day (ages 1–15 d) were calculated from Giudici (2018) and were 12, 15, 17, 23, 33, 45, 60, 85, 110, 145, 180, 225, 267, 320 and 376 g. If foraging birds accrued the correct amount of food for themselves and their chicks before 7 h had elapsed, they returned to their nests, whereas if foraging birds failed to obtain the amount of food to be allocated to chicks within the foraging time, the chicks received correspondingly less food. If the foraging success precluded any energy gain beyond  $E_{\text{ideal}}$  for chicks for more than 3 d, the chicks were considered to have died. The Poisson model and renewal model using the empirical distribution of prey encounter were run from hatching to chick ages of 15 d. For each animal, we compared the output of 100 simulations of the amount of energy obtained to feed day-old chicks in the Poisson model with 100 simulations that used a renewal process using the empirical distribution for the inter-prey capture times. Additionally, for each animal, we compared the total amount of energy obtained during a 15 d period under both inter-prey capture time scenarios. Comparisons were performed by means of Mann-Whitney tests using the function ‘wilcox.test’ in the ‘stats’ package (R Core Team 2019).

### 3. RESULTS

#### 3.1. Inter-individual variation in prey encounter rates

We did not observe any obvious differences between camera-equipped birds and unequipped conspecifics, and all of our birds fed, many extremely well. However, we have no independent assessment

of the extent to which our camera technology might have compromised the ability of equipped birds to forage. We note that the issue of device effects is complex and difficult, if not impossible, to preclude (cf. Vandenabeele et al. 2015), so our results should be considered with this in mind. That apart, our study confirmed that female imperial shags feed on 2 major prey types: *Ribeiroclinus eigenmanni*, ‘small’ prey items which contribute little to the overall mass of food ingested, and *Raneya fluminensis*, ‘large’ prey items, which constitute the major mass component of the diet (Table 1). There was significant variation between individuals in the proportion of these 2 prey types caught ( $\chi^2_{10} = 26.89$ ,  $p = 0.003$ ), and converting the distributions of times between all prey encounters for individuals into probabilities of prey encounter over time,  $P_s$  (where  $P_s = 1/\text{mean prey encounter time}$ ), highlights the substantial differences in prey ingestion probabilities between individuals (Table 1).

In the event that birds take prey with a constant probability of success per unit time, we would expect the times between successful prey encounter frequencies to have an exponential distribution with parameter  $1/P_s$ , where  $P_s$  is the probability of encountering prey per unit time (Table 1). In fact, we found that only 2 of the 11 birds had distributions of prey encounter times that were indistinguishable from the corresponding exponential distribution. Indeed, while the remaining 9 had visually good fits to an exponential distribution (see Fig. S2 in the Supplement) and combined distributions of inter-prey encounter times across all individuals also had ostensibly (visually) an excellent fit to the exponential distribution (Fig. 2), the summary data produced a distribution that also failed the test of an exponential distribution (Lillefors-corrected Kolmogorov-Smirnov test,  $D = 0.19$ ,  $p < 0.01$ ).

Table 1. Probability of catching prey items per second ( $P_s$ ) and proportion of small (*Ribeiroclinus eigenmanni*) and large (*Raneya fluminensis*) prey items caught by different individual imperial shags

Bird ID	$P_s$ all	$P_s$ small	$P_s$ large	Proportion small	Proportion large	N small	N large	N total
B1	0.0061	0.004	0.0022	0.65	0.35	51	27	78
B2	0.0027	0.0008	0.0019	0.31	0.69	14	31	45
F1	0.0025	0.0016	0.0011	0.58	0.42	14	10	24
F3	0.0099	0.0052	0.0048	0.53	0.47	97	86	183
J1	0.0052	0.003	0.0022	0.59	0.41	24	17	41
J2	0.0034	0.002	0.0015	0.57	0.43	34	26	60
L1	0.0051	0.0022	0.0034	0.34	0.66	22	43	65
L2	0.003	0.0014	0.0019	0.38	0.62	13	21	34
P1	0.0087	0.0049	0.0042	0.56	0.44	42	33	75
P2	0.011	0.0055	0.0055	0.5	0.5	52	52	104
P3	0.0092	0.005	0.0042	0.54	0.46	28	24	52

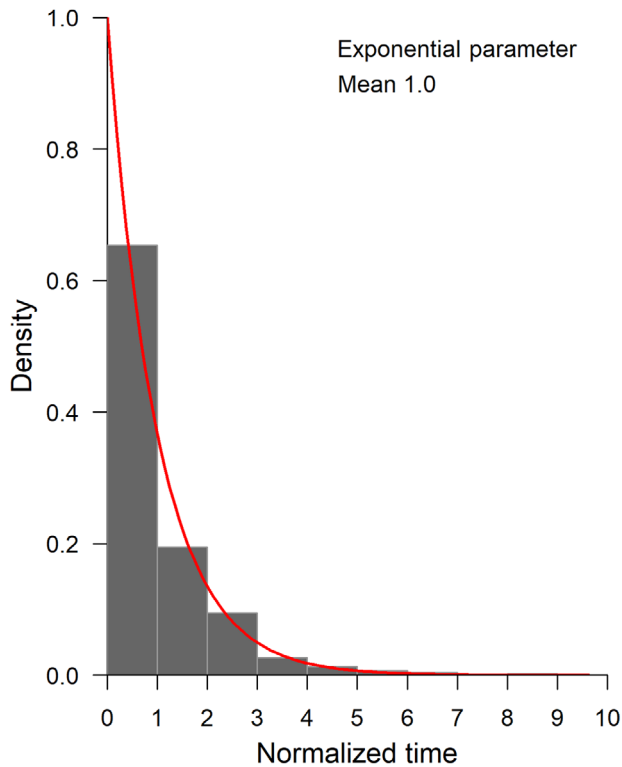


Fig. 2. Frequency distribution of the searching times between prey encounters ( $n = 750$ ) summarized for 11 female imperial shags foraging for themselves and their chicks. The line depicts the expected trend if each individual foraged randomly according to a constant probability of success per unit time ( $P_s$ )

Against this, our simulations of the Poisson model and the renewal model using the empirical distribution showed that, for day-old chicks, the amount of energy adults acquired did not differ between approaches (Table 2). For runs conducted for the first

15 d of chick-rearing, there was no significant difference between the Poisson model and that using the empirical distribution for 8 of 11 birds (73%) (Table 2). Of the remaining 3 individuals, 2 were predicted to bring in more food for their chicks using the Poisson model than the empirical distribution, and 1 was predicted to bring in less food for its chicks using the Poisson model than the empirical distribution.

### 3.2. Effects of probabilistic prey encounter rates on food acquisition and chick provisioning

Incorporating the  $P_s$ -values into a probabilistic foraging model that accounts for the power use during foraging, the power use during all other (non-foraging) activities, the energetic values of large and small prey and the energetic needs of a 2-chick brood showed considerable variation between individuals in the distribution of probable times needed for birds to balance energy expenditure with gain (Fig. 3). Notably, the variation in foraging duration increased with decreasing  $P_s$ -values (cf. Table 1 and Fig. 3). The effects of likely individual energy acquisition trajectories become clear when body energy levels are modelled for a number of individuals over the course of a single day, with the increased variability in the rate of energy acquisition associated with low  $P_s$ -values resulting in greater variability in foraging duration (Fig. 4). Expanding this process across time so that energetic successes or failures over 1 foraging period (and day) are incorporated across the next foraging period (and day) against a backdrop of increasing brood energy needs, indicates that imperial shags with the lowest  $P_s$ -values would not deliver the

Table 2. Comparison of the energy acquired by imperial shags for day-old chicks and for the first 15 d of the chick-rearing period according to whether the duration between captures was exponentially distributed following a Poisson distribution or based on the empirical data. The mean energy values displayed stem from the outcome of 100 simulation runs. The Wilcoxon test statistic ( $W$ ) is shown with the corresponding p-value. Significant p-values ( $p < 0.05$ ) are highlighted in **bold**

Bird ID	Energy for day-old chicks (kJ)				Cumulative energy for 15 d (kJ)			
	Exponential	Empirical	W	p	Exponential	Empirical	W	p
B1	66.38	71.73	5702	0.09	8510	8595	6574	<b>0.0001</b>
B2	64.36	61.90	4503	0.23	8528	8575	5597	0.15
F1	-354.31	-393.08	4722	0.50	-28461	-30342	4588	0.31
F3	70.41	68.41	4748	0.54	8661	8647	4653	0.40
J1	63.00	65.28	5327	0.43	8607	8613	5046	0.91
J2	8.65	16.47	4897	0.80	7161	6838	4040	<b>0.02</b>
L1	71.10	70.97	4955	0.91	8632	8646	5534	0.19
L2	67.05	66.08	4803	0.81	8623	8545	3077	<b>0.0001</b>
P1	70.34	69.00	4811	0.65	8649	8638	4724	0.50
P2	64.67	64.91	4897	0.80	869	8648	4887	0.78
P3	74.84	74.03	4824	0.67	8647	8654	5211	0.61

energy needed for appropriate chick growth (Fig. 4). Using the full spectrum of the determined  $P_s$ -values for our studied birds and the proportions of 'small' to 'large' prey (Table 1) to predict the supply of food to the chicks of given ages, indicates how the probabilistic food found interacts with that needed by the brood (Fig. 5a–c). This shows that the numbers of birds failing to supply the necessary energy is predicted to increase with chick age, although adults failing on any particular day can sometimes make up for the deficit on the following day (Fig. 5d).

#### 4. DISCUSSION

Our data on the intervals between prey encounters by imperial shags provides equivocal information on whether the process of prey acquisition is probabilistic with constant  $P_s$  over time, and the extent to which it matters. On the one hand, only 18% of the birds had distributions that were statistically indistinguishable from a Poisson model and, although the combined results of all individuals seemed to provide a good fit for an exponential distribution (Fig. 2), this too was significantly different from that expected from a Poisson model. Against that, the apparently small difference between the Poisson model and the model using empirical data produced no difference in predicted food accrued by all birds (100%) foraging for day-old chicks and no significant difference in food accumulated by 73% of birds foraging over 15 d for their chicks (Table 2), suggesting that a Poisson model is a reasonable approximation to describe the accumulation of energy by our shags. Of the 27% of birds that were predicted to accrue significantly different amounts of food between the Poisson model and the model using the empirical distribution, two-thirds were predicted to do worse than the Poisson model while one-third (1 bird) was predicted to do better than the Poisson model. This does not make a compelling case for our birds having a prey encounter time distribution that outperforms the Poisson model, either for the 3 individuals bring-

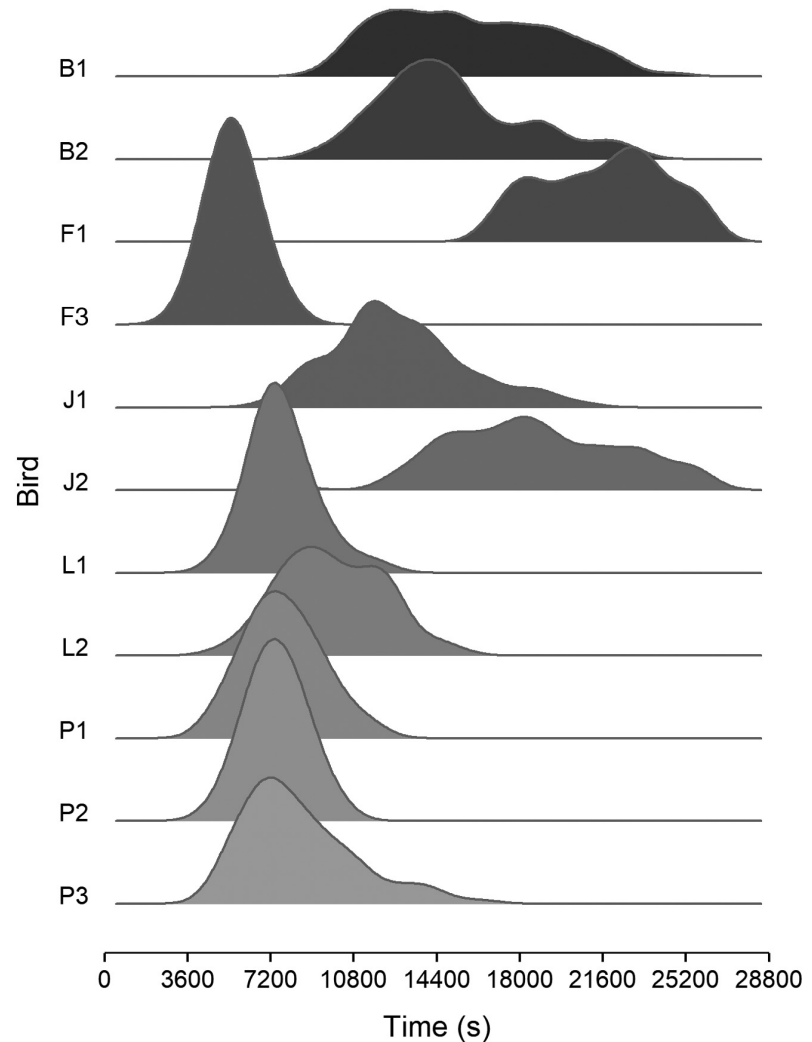


Fig. 3. Distributions of times needed for imperial shags to balance their energy budget by foraging for themselves and their brood (consisting of 2 one-day old chicks) according to the 11 different probabilities of catching prey as shown in Table 1 (each distribution shows the outcome based on 100 runs)

ing in different amounts of food for the chicks over 15 d or for the birds in general.

We suggest that the small differences between our empirical prey encounter time distributions and the Poisson model may be due to varying prey densities (patchiness) along the underwater tracks of birds, which result in varying  $P_s$ -values over time, although much more extensive work will be needed to test this hypothesis. Indeed, although the statistics have ruled out Poisson processes operating for  $P_s$ -values over the scale of the foraging trip of birds, we cannot preclude that this is not the case within presumed patches. Importantly though, the food acquisition consequences of the differences between the Poisson model and empirical based model are trivial, which makes a good case for us using a Poisson-based theo-

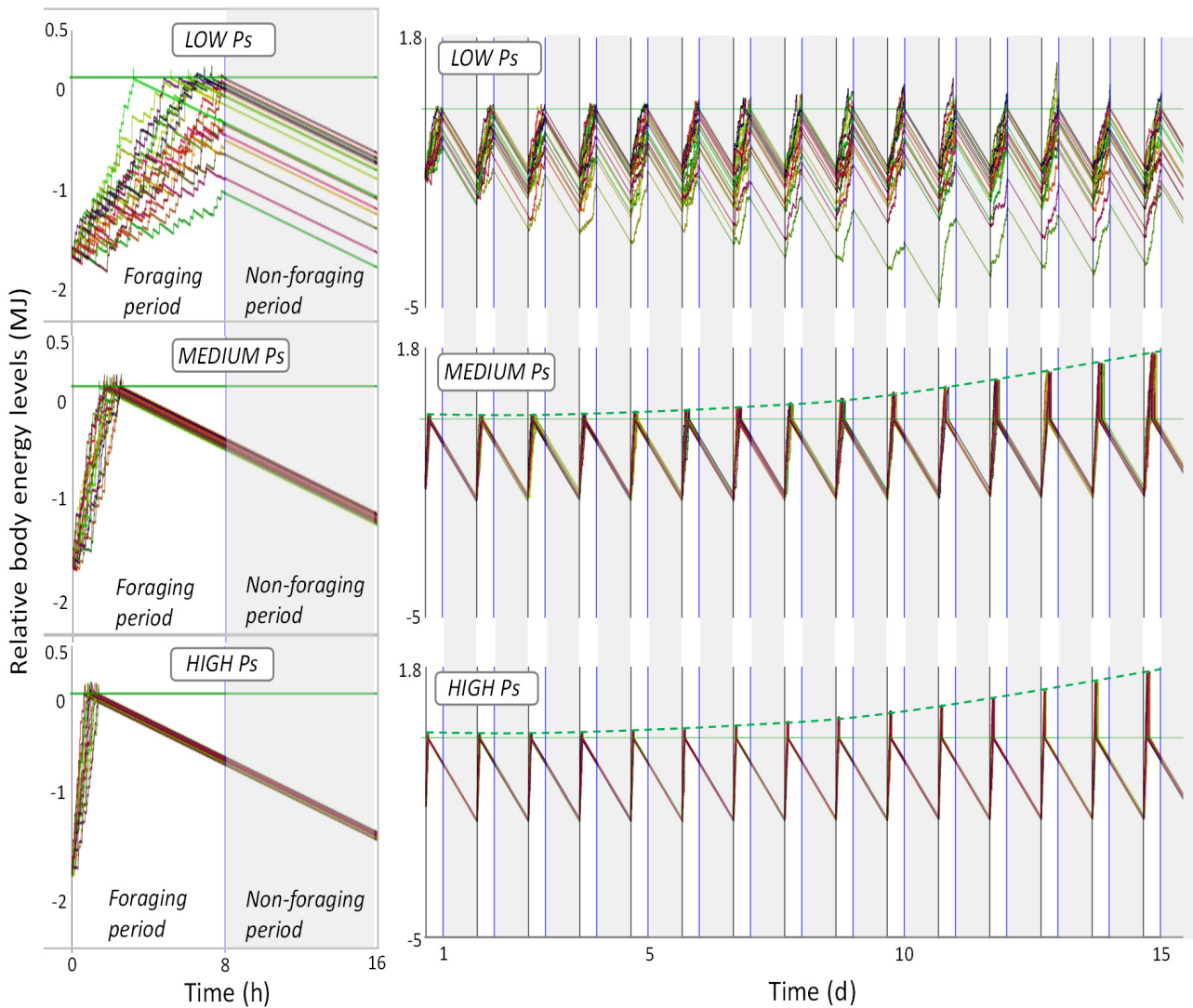


Fig. 4. Probabilistic energy balance of imperial shags (for 20 runs per case) foraging for themselves and their brood with 3 different probabilities of catching prey (low, where overall  $P_s = 0.001$ ; medium,  $P_s = 0.003$ ; high,  $P_s = 0.0055$ ; cf. Table 1), illustrated for 1 d (left column) and 15 d (right column). Medium and high  $P_s$ -value birds easily recoup depressed energy levels stemming from non-foraging periods (where individual lines cross the horizontal green line) and for their chicks (dashed green line – chick feeding is represented by the extent of the vertical drop down to the optimal adult level – horizontal green lines) although medium  $P_s$ -value birds have greater variability. Birds with low  $P_s$ -values show the greatest variability, and this increases over time, with many individuals unable to balance energy expenditure with gain for themselves and/or for their brood

retical underpinning for our modelling, and, critically, these differences are trivial compared to the inter-individual differences in foraging success (Table 1).

Indication that imperial shags operate in a foraging environment that can be modelled by Poisson processes has important implications for our understanding of how their populations (and those of other animals subject to similar constraints) are expected to fare under changing prey abundance scenarios (cf. Fayet et al. 2021). Notably, our framework has been purported to link food plentifulness and reproductive

output (Wilson et al. 2018), something postulated over 70 yr ago (Lack 1954). What is not clear from this work is why some individuals have markedly higher  $P_s$ -values than others (cf. van Daalen & Caswell 2017) despite foraging in the same place (Quintana et al. 2011) and at the same time (cf. Caldow et al. 1999, Stillman et al. 2000, Harris et al. 2013).

We postulate that such successful individuals must adopt tactics, or do so by chance, that effectively lead to them having better odds in their searches than others, and there are a number of factors that could



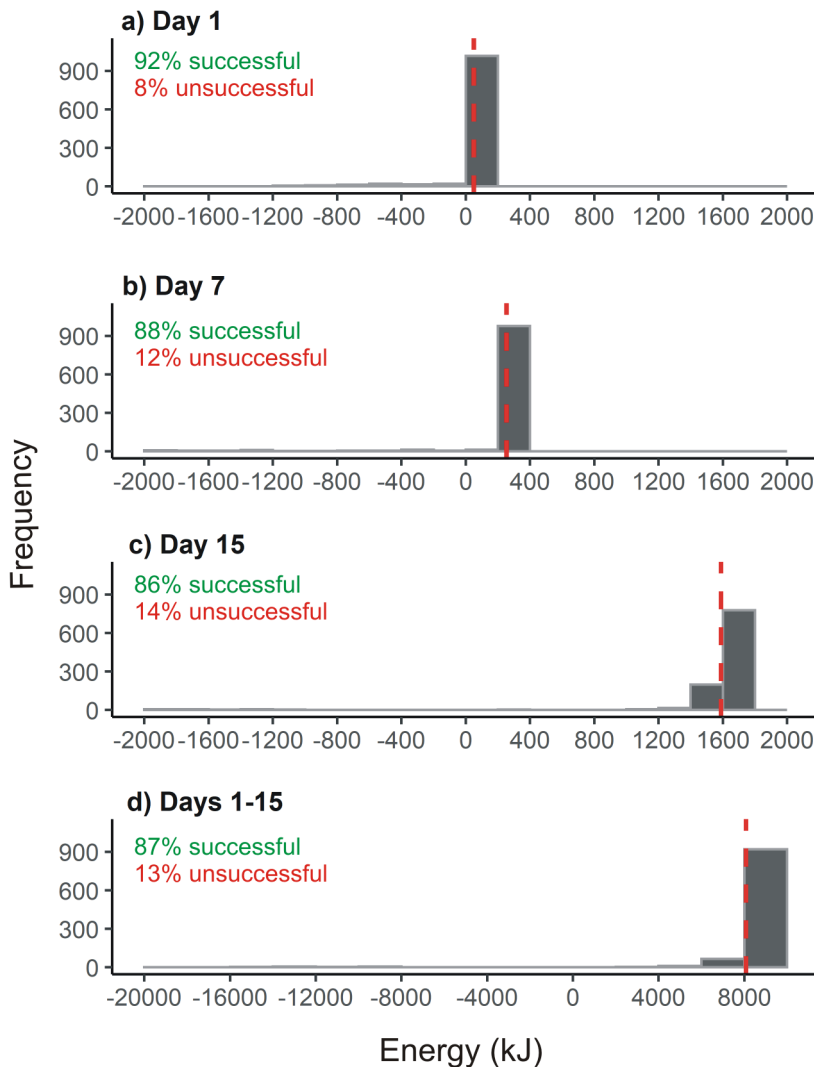


Fig. 5. Probabilistic energy available to feed 2-chick broods within a population of imperial shags displaying the  $P_s$ -values determined in this study (Table 1) for (a–c) different chick ages (in days) and (d) an extended time period. The percentage of the population harvesting the requisite amount of food for each interval is shown in green, while the percentage failing is shown in red. The dashed red line shows the energy threshold, to the right of which normal chick growth is maintained. Note that the percentage of successful birds across the full 15 d period is higher than any single day because birds that failed on any one day could often make up the deficit on the next day. To simulate this scenario, 100 runs were undertaken for each of the  $P_s$ -values shown in Table 1 before results were combined

help explain this. For example, during any single foraging trip, broad levels of food patchiness may play a role (Benhamou 1992, Weimerskirch et al. 2005); some individuals might rely more on conspecifics to locate prey patches and/or indicate which areas to avoid because they are depleted or unproductive (e.g. Boyd et al. 2016), or they may choose to leave unprofitable patches judiciously so as not to waste time or energy where prey are rare (Stephens &

Krebs 1986). Differences in individual morphology might also modulate foraging success under certain conditions (Schröder et al. 2016, De Pascalis et al. 2020), while another possibility is that some individuals may be more efficient at handling prey than others (Paszkowski & Moermond 1984), except that this typically takes such a small fraction of the dive cycle duration that it is unlikely to affect inter-individual differences. Alternatively, since the most successful birds in terms of rate of energy gain are those that have the greatest success with encountering large prey (e.g. individuals F3, P2 and P3), these birds may have search images (sensu Tinbergen 1960) that focus resources on these prey. Otherwise, although all individuals forage in the same general area (Quintana et al. 2011), more successful birds may selectively forage in local patches where prey density is higher (Grémillet et al. 2004), possibly basing decisions on previous experience. Certainly, there is evidence among some animals that older individuals benefit from their greater knowledge (Lescroël et al. 2019, cf. Snyder et al. 2021). Finally, there is also the possibility that some individuals, perhaps because they are ‘bolder’ and more likely to engage in risk-taking behaviour, benefit disproportionately (cf. Snyder & Ellner 2018), specifically when their boldness enhances their  $P_s$ -values, although those same individuals may suffer disproportionately when their boldness reduces these values (Harris et al. 2020). To examine this, and many of the other possibilities outlined above, we would have to monitor

prey-catching successes in specific individuals over multiple foraging trips, and ideally over years. Critical is the extent to which particularly successful individuals in the present study maintain this success compared to others over multiple foraging trips because this would do much to help separate elements of random prey encounter (such as happening to alight in a large productive patch) from tactics that enhance prey acquisition in a variable environment.

Whatever the mechanism by which some individuals enhance their success, the specific value of  $P_s$  has profound implications for reproductive success because (1) during any one foraging trip, the variance in body energy levels across the population increases over time, being greater in animals with low  $P_s$ -values, and (2) this trend continues from one day to the next in birds that have not reached their appropriate energy gain in the previous day. This is because, after foraging, these individuals start the next day with a greater energy deficit than birds that were more successful (Fig. 4). Thus, poor foraging luck and/or bad tactics on one day can have knock-on consequences for subsequent periods.

Darwinian selection necessitates differential competencies between individuals, and any randomness in a food-finding scenario needs to incorporate this (van Daalen & Caswell 2017). In this respect, imperial shags may be operating within a framework whereby the probabilities of foraging success vary over time and space and in a number of other respects (e.g. Caswell 2019). Since the variation in individual heterogeneity will produce individuals that can enhance their chances of breeding successfully (Jenouvrier et al. 2018), in part by judicious tactics in terms of where, when and how to forage as well as via traits (Schröder et al. 2016, De Long et al. 2021), there is a mechanism which allows selection pressures to operate in a world where food-finding might have aspects dependent on luck (Fay et al. 2018). In short, given the critical interplay between traits, tactics and luck, it would seem that the most successful shags in our study will be those birds that forage in a manner that maximizes their prey encounter chances, even within an environment where prey may be encountered at random within and between patches.

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## Appendix.

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