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1 **Go with the flow: water velocity regulates herbivore foraging decisions in river catchments.**

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21 Running title: Herbivore foraging decisions

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23 **Abstract**

24 Foragers typically attempt to consume food resources that offer the greatest energy gain for the least cost,
25 switching between habitats as the most profitable food resource changes over time. Optimal foraging models
26 require accurate data on the gains and costs associated with each food resource to successfully predict temporal
27 shifts. Whilst previous studies have shown that seasonal changes in food quantity and quality can drive habitat
28 shifts, few studies have shown the effects on habitat choice of seasonal changes in metabolic foraging costs. In
29 this study we combined field and literature data to construct an optimal foraging model to examine the effect of
30 seasonal changes in food quantity, food quality and foraging costs on the timing of a switch from terrestrial to
31 aquatic habitat by non-breeding mute swans (*Cygnus olor*) in a shallow river catchment. Feeding experiments
32 were used to quantify the functional response of swans to changes in aquatic plant biomasses. By sequentially
33 testing alternative models with fixed or variable values for food quantity, food quality and foraging cost, we
34 found that we needed to include seasonal variance in foraging costs in the model to accurately predict the
35 observed habitat switch date. However, we did not need to include seasonal variance in food quantity and food
36 quality, as accurate predictions could be obtained with fixed values for these two parameters. Therefore, the
37 seasonal changes in foraging costs were the key factor influencing the behavioural decision to switch feeding
38 habitats. These seasonal changes in foraging costs were driven by changes in water velocity; the profitability of
39 aquatic foraging was negatively related to water velocity, as faster water required more energy to be expended
40 in swimming. Our results demonstrate the importance of incorporating seasonal variation in foraging costs into
41 our understanding of the foraging decisions of animals.

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49 **Introduction**

50 Explaining the spatiotemporal patterns of animal diet and distribution is a central challenge facing ecologists.
51 The most common explanation holds that foragers should attempt to select the habitat and diet that allow them
52 to maximise their intake rate of energy and nutrients over time whilst minimising metabolic foraging costs and
53 risk of exposure to harmful stimuli (*e.g.* toxins) and predation (Stephens and Krebs 1986; Newman et al. 1995;
54 Killen et al. 2007). The most profitable food resource is that which yields the greatest net energy gain (gain
55 minus cost). The predictions of optimal diet theory have been upheld in a range of different field tests (*e.g.*
56 Owen-Smith and Novellie 1982; Nolet et al. 2001; Babin et al. 2011). The theory has proven particularly robust
57 for animals which feed on immobile prey, such as herbivores consuming plant tissues (Sih and Christensen
58 2001). Three key factors can determine what the most profitable diet should be, and consequently where the
59 animals should feed; food quantity, food quality and foraging costs (Stephens and Krebs 1986). Increases in
60 both the quantity and nutritional quality will increase the profitability of a food resource, making it more
61 attractive to foragers (Owen 1972; Owen-Smith and Novellie 1982; Illius et al. 1999). In contrast, increased
62 foraging costs lower the profitability of a food resource. Foraging costs may be direct costs such as the energy
63 expenditure required to search for, capture and consume a prey item, or indirect costs such as increased
64 predation risk (Stephens and Krebs 1986).

65 Optimal foraging models, which calculate the relative gains and costs associated with different available diets
66 and habitats, have proven to be a useful tool to successfully predict forager diet and habitat choice (Owen-
67 Smith and Novellie 1982; Newman et al. 1995; Inger et al. 2006). However, to yield accurate predictions such
68 models require accurate data on the food quantity, food quality and foraging costs that foragers face (Wilson et
69 al. 2012). Many models use fixed values of food quantity, food quality and foraging costs, and thus neglect
70 temporal variance in such parameters. Previous studies have examined the effects of seasonal variance in the
71 quantity and quality of different food resources on animal foraging decisions (Prins and Ydenberg 1985;
72 Vickery et al. 1995; Nolet et al. 2001). However, few studies to date have demonstrated a habitat shift caused by
73 seasonal changes in metabolic foraging costs. Indeed, most studies assume that the metabolic costs of foraging
74 on a given food resource are fixed over time. This is despite the potential for large seasonal variations in
75 metabolic foraging costs between different habitats. There are many species which switch between different
76 foraging habitats, such as those that switch between aquatic and terrestrial habitats, lentic and lotic habitats, or
77 aerial and ground habitats (Prange and Schmid-Nielsen 1970; Sherer and Wunder 1979; Clausen et al. 2012).

78 Therefore studies are needed to explore the influence of seasonal changes in food quantity, food quality and
79 foraging costs on the behavioural decisions of foraging animals.

80 Herbivorous waterfowl (Order: Anseriformes) within shallow river catchments move seasonally between
81 feeding in the river itself to adjacent terrestrial pastures, and thus offer an ideal system with which to examine
82 the factors which influence forager movements (Mason and Macdonald 2000; Wood et al. 2013a). Seasonal
83 changes in the relative profitability of aquatic and terrestrial food resources are believed to cause a diet (and thus
84 habitat) shift in non-breeding mute swans (*Cygnus olor* Gmelin, 1789) (Wood et al. 2013a). These swans exhibit
85 a seasonal switch between foraging in the river on submerged aquatic plants in summer and autumn, and
86 foraging in terrestrial pasture fields on pasture grasses in winter and spring (Wood et al. 2013a). Swans enter the
87 river between April and May, and may cause localised grazing damage thereafter (Wood et al. 2012a; Wood et
88 al. 2013b). In shallow rivers foraging costs may be regulated by water velocity, which determines the energy
89 required for movement. Thus at higher water velocities a forager must expend more energy swimming (Prange
90 and Schmidt-Nielsen 1970; Butler 2000; Bejan and Marden 2006). Indeed, the period when non-breeding swans
91 use the river coincides with the lowest seasonal water velocity values (Wood et al. 2013a).

92 In this study we combined field and literature data with an optimal foraging model to investigate an observed
93 seasonal habitat shift in mute swans. We measured the quantity and quality of the two food resources available
94 to swans, water crowfoot and pasture grass. We estimated the intake rates for water crowfoot by conducting
95 feeding trials, and for pasture grass by allometric scaling of published data. We used published literature and
96 calculated water velocities to estimate foraging costs. Finally, we used an optimal foraging model to examine
97 whether seasonal changes in food quantity, food quality or foraging cost, or a combination of these three factors,
98 explained the observed shift of non-breeding mute swans from terrestrial to aquatic habitat. We tested four
99 alternative hypotheses; swan foraging profitability would be determined by seasonal changes in (*H1*) food
100 quantity, (*H2*) food quality, (*H3*) foraging costs, or (*H4*) a combination these factors.

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102

103 **Methods**

104 *Study system*

105 Our study system was a mesotrophic chalk river catchment, the River Frome (Dorset, UK), from Maiden
106 Newton (50°46'N, 02°34'W) 44 km downstream to West Holme (50°41'N, 02°10'W). The main river channel
107 is dominated by the aquatic plant stream water crowfoot (*Ranunculus penicillatus* ssp. *pseudofluitans* (Syne)
108 S.D. Webster) (Wood et al. 2012a). The river is typically bordered by terrestrial pasture fields dominated by
109 perennial ryegrass (*Lolium perenne* L.), creeping bentgrass (*Agrostis stolonifera* L.), and Yorkshire fog (*Holcus*
110 *lanatus* L.), which frequently become water-logged during winter (Wood et al. 2013a). Predation risk for adult
111 swans is very low and does not differ between habitat types (< 3 % of all mortality; Brown et al. 1992).

112

113 *Food quality*

114 We selected 20 river sites on the main channel of the River Frome that were characteristic of the river in terms
115 of morphology, hydrology and plant community. Pasture grass was repeatedly sampled from the pasture field
116 adjacent to each of the river sites; however, at two sites there was no pasture field and thus we sampled from 20
117 river sites and 18 pasture fields. Quantitative samples of water crowfoot ($n = 10$ cores per month; Wood et al.
118 2012a) and pasture grass ($n = 5$ cores per month; Wood 2012) were taken monthly from March to September
119 2010 using a 0.00785 m² hand corer. Full details of the methodology, as well as the results for water crowfoot,
120 are given in Wood *et al.* (2012a). For pasture grass, sward height (± 0.5 cm) was measured at the centre of each
121 core. All samples were bagged, labelled and taken to the laboratory, where non-plant material and excess water
122 were removed, before fresh mass (± 0.01 g) was measured on a Sartorius PT120 balance (Sartorius GmbH,
123 Germany). The plant sample was then dried to constant mass at 60 °C in a Heraeus Kelvitron T oven (Thermo
124 Fisher Scientific, Loughborough, UK), reweighed and the dry matter (DM) biomass (± 0.01 g) was recorded.

125 We measured the nutritional quality of water crowfoot and pasture grass, in terms of energy content, at four of
126 our sites each month between March and September. Randomly selected samples ($n = 3$) from four river and
127 four adjacent field sites were ground for 300 s at 25 Hz in a Retsch MM200 Ball Mill (Retsch GmbH,
128 Germany). This sub-sampling approach was used as it was not economically viable to analyse samples from all
129 sites; these four sites were selected as they were characteristic of the catchment in terms of land use, sediment
130 composition and plant community. Prior to analyses samples were redried at 105 °C for three hours in a
131 Gallenkamp Prime Oven (Weiss Gallenkamp, Loughborough, UK). To determine energy (kJ g⁻¹) content $0.20 \pm$
132 0.01 g DM of each sample was analysed using a 1109 semi-micro oxygen bomb and 6200 Oxygen Bomb
133 Calorimeter (Parr Instrument Company, USA).

134 To calculate the plant metabolizable energy content for each plant species we used the formula:

$$135 \quad ME = GEI - FEO / GMI,$$

136 where ME was the plant metabolizable energy content ($\text{kJ g}^{-1} \text{DM}$), GEI was the swan daily gross energy intake
137 (kJ), FEO was the swan daily faecal energy output (kJ) and GMI was the swan gross dry matter intake (g). Swan
138 GMI was calculated as the product of swan daily foraging time (FT) and swan intake rate for that plant species.
139 FT was estimated at 27562 s (31.9 % of day) and 49766 s (57.6 % of day) when feeding on water crowfoot and
140 pasture grass respectively, based on the time budget study reported in Wood (2012). For water crowfoot we
141 assumed an intake rate of $0.032 \text{ g DM s}^{-1}$ based on the functional response for biomass and gross energy content
142 values of $297.8 \text{ g DM m}^{-2}$ and $13.4 \text{ kJ g}^{-1} \text{DM}$ respectively. For pasture grass we assumed an intake rate of 0.016
143 g DM s^{-1} based on the functional response for biomass and gross energy content values of $439.7 \text{ g DM m}^{-2}$ and
144 $15.8 \text{ kJ g}^{-1} \text{DM}$ respectively. GEI for swans feeding on each plant species was estimated as the product of GMI
145 and gross energy content for that species. We calculated as FEO as:

$$146 \quad FEO = ((FT \cdot FR) \cdot FM) \cdot FE,$$

147 where FT was daily foraging time (s), FR was the rate of excretion whilst foraging (droppings s^{-1}), FM was mass
148 per dropping (g), and FE was the energy content per dropping ($\text{kJ g}^{-1} \text{DM}$). FR was estimated from the
149 allometric equation for waterfowl provided by Hahn *et al.* (2008): $\log_{10} FM = 10^{2.130} * M^{0.3065}$, which we
150 converted to droppings per second. M was species body mass (10800 g: Kear 2005). Mean \pm 95 % CI values for
151 FM were estimated at 8.5 ± 3.3 and $7.4 \pm 1.9 \text{ g DM dropping}^{-1}$ for water crowfoot and pasture grass
152 respectively, based on measurements of 40 faecal samples (20 water crowfoot and 20 pasture grass) collected
153 over the study period, dried and weighed according to the protocol for plant samples. FE was estimated using
154 the bomb calorimetry protocol as for plant samples, which gave mean \pm 95 % CI values for water crowfoot of
155 $9.96 \pm 1.38 \text{ kJ g}^{-1} \text{DM}$ ($n = 9$) and for pasture grass of $12.90 \pm 1.00 \text{ kJ g}^{-1} \text{DM}$ ($n = 9$). Thus we calculated FEO
156 for water crowfoot foraging as 6573 kJ and for pasture grass foraging as 7175 kJ.

157 Thus we calculated the metabolizability, the percentage of energy which is absorbed and is thus biologically
158 available, for each plant species we used the formulae:

$$159 \quad \text{Metabolizability} = (ME / GE) \cdot 100,$$

160 where ME was the plant metabolizable energy content (kJ g^{-1} DM) and GE was the plant gross energy content
161 (kJ g^{-1} DM). Thus metabolizability for water crowfoot was 44 % and for pasture grass was 21 %.

162

163 *Food quantity*

164 Each month the dry matter quantity (g DM m^{-2}) of each food plant, water crowfoot and pasture grass, were
165 estimated as the mean of all samples taken in that month (Wood et al. 2012a). Swans can reach up to 1 m
166 underwater whilst foraging (Owen and Cadbury 1975); as the river depth in our study system rarely exceeds 1 m
167 (Wood et al. 2012a; Wood et al. 2012c), we assumed that 100 % of water crowfoot biomass is available to
168 swans. We estimated mute swan intake rate for pasture grass by allometric scaling of pasture grass functional
169 response reported for other generalist herbivore waterfowl species, whilst the intake rate for water crowfoot was
170 estimated from experimental feeding trials. A pasture grass functional response (*sensu* Holling 1959) of
171 Bewick's swans (*Cygnus columbianus bewickii* Yarrell, 1830), a congener of the mute swan, has been reported
172 by van Gils et al. (2007). Bewick's swan intake rate (I_{Bew} , in g DM s^{-1}) was reported as:

$$173 I_{Bew} = (a \cdot (1.38 \cdot 10^{-3} \cdot H)) / (a \cdot b + (1.38 \cdot 10^{-3} \cdot H)) / 60$$

174 where H was the sward height in cm, and a and b were the bite size and handling time (3.6 and 0.02
175 respectively) derived by van Gils et al. (2007). We modified this equation so that intake rate was expressed for a
176 given pasture grass biomass (B , in g DM m^{-2}) rather than sward height (H , in cm); using the sward height and
177 biomass data from our 18 field sites. We found a significant, positive relationship between mean sward height
178 and biomass for all months at all sites (Linear regression: $F_{1,124} = 211.9$, $p < 0.0001$, $R^2_{adj} = 63\%$). Thus we
179 converted sward height to sward biomass according to the following relationship:

$$180 H = 0.0238 \cdot B$$

181 Wood *et al.* (2012b) demonstrated that pasture grass intake rates scale with the mean body mass of waterfowl
182 species according to the following regression relationship ($R^2_{adj} = 72\%$):

$$183 \text{Log}_{10} I = -4.89 + 0.81 \cdot \text{Log} M$$

184 where M = mean species body mass (g). We used this equation to calculate the relative difference between the
185 pasture grass intake rates of Bewick's ($0.0148 \text{ g DM s}^{-1}$) and mute ($0.0238 \text{ g DM s}^{-1}$) swans, assuming body

186 mass values of 6000 g and 10800 g respectively (Kear 2005). We calculated the intake rate of a mute swan
187 relative to a Bewick's swan as:

$$188 \quad 0.0238 \text{ g DM s}^{-1} / 0.0148 \text{ g DM s}^{-1} = 1.61$$

189 Thus we estimated the intake rate for mute swans feeding on a given pasture grass biomass as:

$$190 \quad I_{Mute} = I_{Bew} \cdot 1.61$$

191 where I_{Mute} and I_{Bew} were the intake rates (g DM s^{-1}) of mute and Bewick's swans respectively.

192 As the functional response for above-ground aquatic plants had not been quantified for any swan species, we
193 conducted feeding trials of mute swans on water crowfoot in November 2009 at Abbotsbury Swannery, Dorset,
194 UK (50°39'N, 02°36'W). Five randomly-selected adult swans, two males and three females, were placed in
195 individual pens (average area = 33.6 m²) consisting of a pond surrounded by a sand embankment. Ages ranged
196 from 3 to 8 years (median 6). For the first six days, each bird was presented with water crowfoot *ad libitum* in
197 0.15 m² black plastic trays, 435 mm (l) x 335 mm (w) x 90 mm (d), in order to acclimatize them to the feeding
198 trial conditions. Fresh water crowfoot was obtained daily from the River Frome at East Stoke (50°41'N,
199 02°11'W), and strands were drawn at random for use in the trials; only healthy strands with leaves present were
200 selected. On the seventh day feeding trials commenced; each bird was presented once per day with a
201 predetermined biomass of water crowfoot in its tray and allowed to feed for 180 ±10 s. Trays were filled with
202 clear water and placed at the shallow edge of the pond. The water crowfoot strands were arranged to cover the
203 largest possible surface area inside the tray in order to maintain a constant foraging area. Each feeding trial was
204 filmed using a tripod-mounted Canon Legria HFS10 HD video camera (Canon Inc., Japan) and all observers left
205 the feeding area to minimise disturbance. After excess water was removed with paper towel, macrophyte
206 biomass was weighed before (R_b) and after (R_a) each trial using a Pesola PTS3000 balance (Pesola AG,
207 Switzerland). Any water crowfoot that had been removed from the tray but not consumed was counted as
208 'wastage' (R_w) and weighed separately. Consumption was calculated as:

$$209 \quad \text{Consumption} = R_b - (R_a + R_w)$$

210 Twelve water crowfoot fresh biomasses, reflecting biomasses reported in field studies, were presented to each
211 bird during the trials; 50 g m⁻², 75 g m⁻², 100 g m⁻², 150 g m⁻², 200 g m⁻², 300 g m⁻², 500 g m⁻², 750 g m⁻², 1000 g
212 m⁻², 1500 g m⁻², 2000 g m⁻², and 3000 g m⁻² (Wood *et al.*, 2012a). Both the order in which each bird received the

213 different macrophyte biomasses, and the order in which each bird was tested each day, were randomised. All
214 individuals had access to grit and water *ad libitum*. As these feeding trials were not considered a procedure, as
215 defined in the Animals (Scientific Procedures) Act 1986, we did not require a Home Office licence.

216

217 *Foraging costs*

218 Mute swan BMR, in Watts (W), was calculated as:

$$219 \text{ BMR} = (\text{VO}_2 \cdot m) \cdot e$$

220 where VO_2 was the consumption of oxygen ($\text{ml O}_2 \text{ g}^{-1} \text{ s}^{-1}$) as reported in Bech (1980), m was mean swan mass
221 (10800 g) as given in Kear (2005), and e was the energy yielded per ml of oxygen consumed ($\text{kJ ml}^{-1} \text{ O}_2$)
222 assuming a conversion of $0.02 \text{ kJ ml}^{-1} \text{ O}_2$ (Nolet et al. 2002). Thus we estimated mute swan BMR as 39 W. We
223 calculated the energetic cost of terrestrial foraging as the multiple of basal metabolic rate (BMR) reported for a
224 congenital species, the Bewick's swan, in Nolet et al. (2002), yielding a mean $\pm 95\%$ CI value of 47 ± 22 W.
225 Whilst BMR increases with mean body mass across species, the metabolic costs of behaviours as a multiple of
226 BMR are consistent between closely related, morphologically-similar species such as mute and Bewick's swans
227 (Bruinzeel et al. 1997). To estimate the energetic cost of aquatic foraging, we calculated the cost of swimming at
228 a given water velocity (v ; m s^{-1}) using the mean relationship between the multiple of BMR (${}_x\text{BMR}$) and
229 standardised swimming speed L (body lengths $^{0.4} \text{ s}^{-1}$; Ware 1978) for barnacle geese (*Branta leucopsis* Bechstein,
230 1803; Nolet et al. 1992), northern mallard (*Anas platyrhynchos* L.; Prange and Schmidt-Nielsen 1970), and
231 tufted duck (*Aythya fuligula* L.; Woakes and Butler 1986), as such data for swans were unavailable (**Figure 1**):

$$232 {}_x\text{BMR} = 1.5 + (-1.2L) + 2.4(L^{0.4})$$

233 Based on our derived mute swan BMR (39 W) and mute swan body length at the water line (0.625 m; Kear
234 2005) we calculated the metabolic cost (FC ; in W) of swimming at a given water velocity as:

$$235 FC = ({}_x\text{BMR}_v \cdot \text{BMR}) + TC,$$

236 where ${}_x\text{BMR}_L$ was the multiple of BMR for a given value of v , and TC was the additional thermoregulatory cost
237 of aquatic foraging. Thus we estimated the relationship between the metabolic cost (FC ; in W) of swimming at a
238 given water velocity (**Figure 1**) as:

239 $FC = (314.9(v^{^2}) - 87.2v + 59.0) + TC$

240 As mute swans and northern mallards are closely related (Order: Anseriformes) they have a highly similar
241 morphology and swimming action. Furthermore, as functionally similar surface-swimming birds both species
242 have the same hull design, a displacement hull, which determines the shape of the relationship between energy
243 expenditure and water velocity (Prange and Schmidt-Nielsen 1970). Therefore we expected an equivalent BMR-
244 swimming speed relationship for both species. Daily mean water discharge ($m^3 s^{-1}$) measurements between 1st
245 March and 31st September 2010 were provided by the Environment Agency for the East Stoke gauging station
246 (station number 44001; 50°41'N, 02°11'W), from which daily mean water velocity ($m s^{-1}$) values were
247 calculated for this period (**Figure 2**). Because water discharge, velocity, and channel cross sectional area (width
248 multiplied by depth) are interrelated according to the relationship, discharge = velocity · cross sectional area, we
249 carried out a back calculation of velocity that was based on the standard technique used to derive depth-
250 discharge relationships for gauging station rating curves, although in this instance velocity, not depth was
251 derived (Bovee and Milhouse 1978; Gordon 1992). River cross sections were available for East Stoke, recorded
252 using the methods described in Wood et al. (2012c). Only four cross sectional areas were available and hence
253 some caution was necessary in interpreting the results, however it is known that three points are sufficient to
254 extrapolate within the range 40 – 250 % of calibrated flow (Bovee and Milhouse 1978). Mean cross sectional
255 velocity (v , in $m s^{-1}$) was calculated according to the formula:

256 $v = a \cdot (1 - \exp(-b \cdot Q))$,

257 where Q was the mean discharge ($m^3 s^{-1}$), whilst a (1.44; Wood et al. 2012c) and b (0.12; Wood et al. 2012c)
258 were the intercept and slope of the relationship between cross-sectional area and discharge. The efficacy of the
259 relationship was tested and confirmed using velocity and depth data from a flow accretion survey carried out at
260 the River Frome at East Stoke (50°41'N, 02°11'W; Arnott *et al.* 2009), and monitoring data collected as part of
261 the Lowland Catchment Research programme (LOCAR) funded by the Natural Environment Research Council,
262 UK.

263 We assumed that BMR did not vary with temperature for terrestrial foraging as Bech (1980) demonstrated that
264 mute swans are thermoneutral in air between 1 and 15 °C, which corresponds with the temperature range within
265 our study system (Wood et al. 2012a). However, animals typically incur an additional thermoregulatory cost
266 when in water compared with terrestrial activity. Jenssen et al. (1989) found that, < 15 °C, the additional

267 thermoregulatory cost (TC ; $W \text{ kg}^{-1}$) to surface-swimming waterfowl varied with temperature according to the
268 equation:

$$269 \quad TC = 1.80 - (0.09 \cdot t),$$

270 where t refers to water temperature ($^{\circ}\text{C}$) and mean mute swan mass equals 10.8 kg (Kear 2005). Jenssen et al.
271 (1989) found no additional thermoregulatory cost at water temperatures above 15 $^{\circ}\text{C}$. We used the mean
272 monthly water temperatures for our study area given in Wood et al. (2012a) to calculate the additional
273 thermoregulatory cost of aquatic feeding for each month. The movement speed required for activity-
274 thermoregulatory heat substitution to occur in a 10.8 kg bird has been shown to be $> 2 \text{ m s}^{-1}$ for the temperature
275 range in our study system (Humphries and Careau 2011). As the water velocity in the River Frome does not
276 exceed 1 m s^{-1} during March to September (**Figure 2**), we assumed that no activity-thermoregulatory heat
277 substitution occurred.

278

279 *Foraging models*

280 We used a model to calculate the profitability of a swan foraging in aquatic and terrestrial habitats each month
281 between March and September. We compared these profitability values to predict when swans should switch
282 between habitats, assuming that swans should always feed on the most profitable food resource. In each model
283 the profitability (rate of energy gain, in kJ s^{-1}) of the two food resources was determined by the equation:

$$284 \quad \text{Profitability} = ((FQI \cdot d) \cdot I_{FQn}) - FC,$$

285 where FQI was the gross energy content ($\text{kJ g}^{-1} \text{ DM}$), d was the digestibility as a proportion of the gross energy
286 content, I_{FQn} was the intake rate (g DM s^{-1}) for a given biomass value of FQn (g DM m^{-2}), and FC was the
287 metabolic cost of foraging (kJ s^{-1}).

288 We sequentially tested all eight combinations of models of fixed and variable values for food quantity (FQn ; g
289 DM m^{-2}), food quality (FQI ; $\text{kJ g}^{-1} \text{ DM}$) and foraging costs (FC ; kJ s^{-1}). Where parameters were variable, the
290 mean value for each month was used. Where parameters were fixed, the mean value for the March to September
291 was used. This approach allowed us to examine how the profitability of the two food resources changed under
292 conditions of fixed or variable food quantity, food quality and foraging costs, and assess how such changes
293 affected the food resource swans were predicted to exploit. The ‘best’ model was the one which required the

294 fewest parameters to successfully predict that the observed habitat switch would occur between April and May
295 (**Figure 3**; Wood et al. 2013a), as this model was the most parsimonious in terms of data required.

296

297 *Sensitivity analysis*

298 To quantify how sensitive our best model predictions were we performed a sensitivity analysis following the
299 one-at-a-time method of local sensitivity analysis. For each parameter in our best model we (i) increased the
300 value in 10 % increments from 0 % to 100 % and (ii) decreased the value in 10 % increments from 0 to – 100 %;
301 the percentage increase and decrease at which the model no longer correctly predicted the habitat switch date.
302 This process yielded for each parameter the range of values within which our model predictions are likely to be
303 robust.

304

305

306 **Results**

307 *Food quality*

308 Limited between-month variance was found in the mean (\pm 95 % CI) gross energy content of water crowfoot
309 (13.4 ± 0.2 kJ g⁻¹ DM) and pasture grass (15.8 ± 0.3 kJ g⁻¹ DM) (**Figure 5b**). No consistent seasonal trend in
310 energy content was observed for either plant.

311

312 *Food quantity*

313 When foraging on water crowfoot swan intake rate (I , in g DM s⁻¹) increased with food density (B , in g DM m⁻²)
314 according to the relationship $I = (0.0031 (\pm 0.0006) \cdot B) / (1 + (0.0934 (\pm 0.0207) \cdot B))$ (**Figure 4**). Water
315 crowfoot biomass exhibited a strong seasonal pattern, increasing from 38.5 g DM m⁻² in March to a seasonal
316 maximum of 576.4 g DM m⁻² in July, declining thereafter (**Figure 5a**). Pasture grass biomass showed a gradual
317 but uneven increase across the study period, rising from 333.8 g DM m⁻² in March to 566.9 g DM m⁻² in
318 September (**Figure 5a**). Mean biomass values for the March to September period were 297.8 g DM m⁻² and
319 439.7 g DM m⁻² for water crowfoot and pasture grass respectively.

320

321 *Foraging costs*

322 Mean (\pm 95 % CI) water velocity declined seasonally from 0.98 (\pm 0.02) m s⁻¹ in March to 0.41 (\pm 0.01) m s⁻¹ in
323 September (**Figure 2**). Accordingly, the cost of aquatic foraging declined over the study period from 277 W in
324 March to 75 W in July (**Figure 5c**). The additional thermoregulatory cost of aquatic foraging accounted for a
325 mean of just 2.7 % (range 0.0 to 8.6 %) of the total metabolic cost of aquatic foraging. Additionally, as mean
326 water temperature exceeded the 15.0 °C threshold in June (16.9 °C), July (18.0 °C), and August (15.7 °C), the
327 additional thermoregulatory cost of aquatic foraging was 0 W in these months. The mean foraging cost between
328 March and September was 144 W. However, in all months the cost of aquatic foraging was higher than the cost
329 of terrestrial foraging. The cost of terrestrial foraging was assumed not to vary (47 W).

330

331 *Foraging models*

332 All four models in which foraging costs were a variable parameter correctly predicted that the habitat switch
333 should occur between April and May (**Figure 6**). In contrast, none of the four models in which foraging costs
334 were a fixed value indicated that the relative profitability of aquatic and terrestrial foraging should change. The
335 accuracy of the model predictions was not influenced by whether food quantity or food quality were fixed or
336 variable parameters (**Figure 6**).

337

338 *Sensitivity analysis*

339 For the majority of parameters in our best model (**Figure 6e**) we found large ranges of values over which our
340 model would correctly predict the observed habitat switching date (**Figure 7**); for example six of ten parameters
341 had ranges that spanned at least - 50 % to + 50 %. Large changes in these parameter values were therefore
342 required for the model to generate inaccurate predictions of the habitat switch date. However, our model showed
343 greater sensitivity to four parameters associated with foraging in aquatic habitat; changes of > -20 % or > 30 %
344 in water crowfoot digestibility, water crowfoot energy content, swan functional response for water crowfoot,
345 and the cost of aquatic feeding to swans, resulted in a predicted habitat switch that was too early. Equivalent
346 patterns of sensitivity were detected for models using fixed FC values (**Figure 6d**; **Figure 6f** and **Figure 6g**); in

347 particular, no magnitude of change in any parameter caused a correct prediction (*i.e.* April-May habitat switch)
348 to be made.

349

350 **Discussion**

351 In this study we have demonstrated how a habitat switch by a population of generalist herbivores is regulated by
352 the seasonal change in the metabolic costs associated with foraging. Many previous studies have assumed that
353 such foraging costs were fixed and did not influence seasonal switches between habitats. Our study offers a
354 mechanistic understanding, based on the gains and costs associated with different food resources, of forager
355 shifts between alternative habitats.

356 To accurately predict the date when swans would switch from terrestrial to aquatic foraging, we needed to
357 include seasonal variance in foraging costs in our model. However, we did not need to include seasonal variance
358 in food quantity and food quality, as accurate predictions could be obtained with fixed values for these two
359 parameters. Food quantity in the river increased more steeply than in pasture fields between March and July and
360 therefore could have potentially explained the observed habitat shift; however, the models suggested that these
361 changes in food quantity alone did not affect the relative profitability of the two food resources. The swan
362 functional response to water crowfoot biomass could at least partially explain this; as water crowfoot biomass
363 ranged between 40-580 g DM m⁻² (**Figure 5a**), our functional response curve suggests almost no increase in
364 intake rate over this range. Hence swan intake rate on water crowfoot was almost invariant over the seasonal
365 range of biomass values. Although our study was correlational, the results suggested that the seasonal changes
366 in foraging costs may have been a key factor influencing the decision of the swans to switch feeding habitats,
367 supporting our third hypothesis (*H3*). These seasonal changes in foraging costs appeared to be related to changes
368 in water velocity; the profitability of aquatic foraging was negatively related to water velocity, as faster water
369 required more energy to be expended swimming (Prange and Schmidt-Nielsen 1970; Butler 2000; Bejan and
370 Marden 2006). For this same reason, the costs of non-foraging activities would also be higher in the river
371 compared with the terrestrial habitat. Therefore swans appear to delay switching to the river until the net rate of
372 energy gain whilst foraging compensates for the additional metabolic cost of activities in flowing waters. We
373 did not have the data to examine the reverse shift from river to pasture that has been observed between October
374 and November (Wood et al. 2013b). However, water velocity is known to increase in response to the seasonal
375 increase in precipitation which occurs during this period, which suggests that changes in water velocity may

376 again drive this swan habitat shift later in the year (Wood et al. 2013a). In contrast to some other animals, such
377 as ungulates (Beier and McCullough 1990), inter-habitat differences in temperature and associated
378 thermoregulatory cost had little effect on swan habitat use. Waterfowl have low thermal conductivity due to
379 their dense plumage, which results in low additional thermoregulatory costs for aquatic feeding in temperate
380 regions (Jenssen et al. 1989; van Sanst and Bakken 2006). However, at higher latitudes additional
381 thermoregulatory costs can be much greater due to substantially lower temperatures (Irving et al. 1955; Lefebvre
382 and Raveling 1967).

383 The use of optimal foraging models to investigate animal behaviour and decision making depends on such
384 models yielding predictions for which both the accuracy and sensitivity are known. We demonstrated through a
385 sensitivity analysis that the habitat switch date predicted by the model was robust against changes in the values
386 of the majority of parameters. Whilst the model was more sensitive to a few key parameters, the relatively
387 modest changes required to generate an incorrect prediction may not be achieved in nature. For example, a
388 change of + 30 % in water crowfoot energy content was required to yield an incorrect prediction. However,
389 given that maximum spatial variation in water crowfoot values which we detected was only $\pm 10\%$, our results
390 were likely robust. The large between-individual variation in the functional response of swans feeding on water
391 crowfoot ($\pm 35\%$) did exceed the limit for accurate predictions (+ 30 %); however the exceedance was small
392 and furthermore was the only incidence where the ranges for accurate predictions was exceeded.

393 Knowledge of the energy gains and costs between different habitats permits the construction of energy
394 landscape (sensu Wilson et al. 2012); models which incorporate the spatial variation in energy gains and costs
395 can yield a mechanistic, process-based understanding of decision making in animals, such as habitat selection. If
396 the factors which control animal movements can be understood, such factors might be manipulated to influence
397 the distribution of animals within the landscape. Mechanistic models which can make accurate, robust
398 predictions regarding animal habitat selection and energy balance could therefore be useful tools for wildlife
399 managers. Scenarios where the management of animal distributions may be required include species of
400 conservation concern, species where harvestable populations are desired (e.g. shooting quarry), and pests of
401 agriculture (Sutherland 1998; Gordon et al. 2004; Wood et al. 2013b). In this way the insights of behavioural
402 ecology could be used to inform wildlife management.

403 Our study indicates the importance of comparing values of profitability for food resources in different habitats,
404 with different associated costs, within a landscape. Crucially, where inter-habitat differences in metabolic

405 foraging costs exist, such comparisons must include estimates of the energetic costs of foraging on each food
406 resource, not just the gross gains. Highly mobile foragers such as waterfowl can track the most profitable food
407 resource as seasonal changes in foraging costs occur. Our results demonstrate that, at least where strong
408 seasonal changes in foraging costs occur, these changes should be included in calculations of the profitability of
409 different food resources available to foragers to allow the construction of an energy landscape.

410

411

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421

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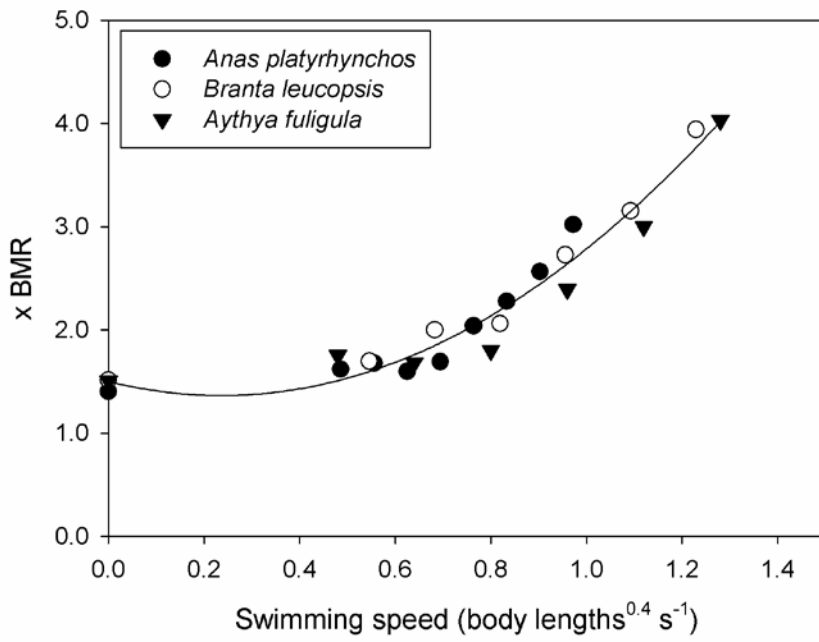
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533 **Figure 1:** The cost of swimming at a given water velocity independent of water temperature, expressed as the
534 multiple of BMR and the metabolic cost in W.

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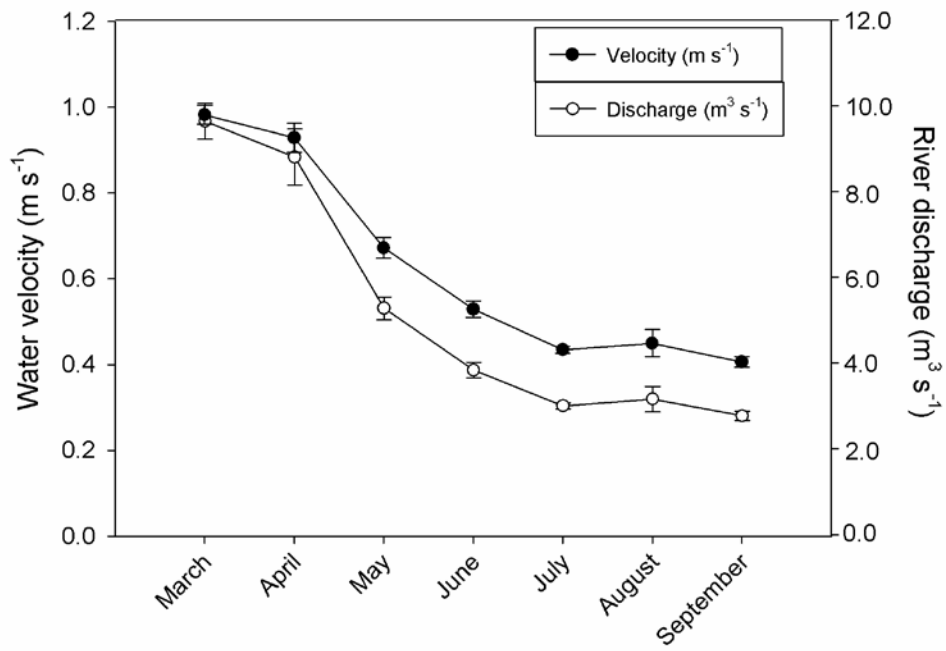
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552 **Figure 2:** Monthly changes in mean \pm 95 % CI gauged discharge and calculated velocity for the study area.

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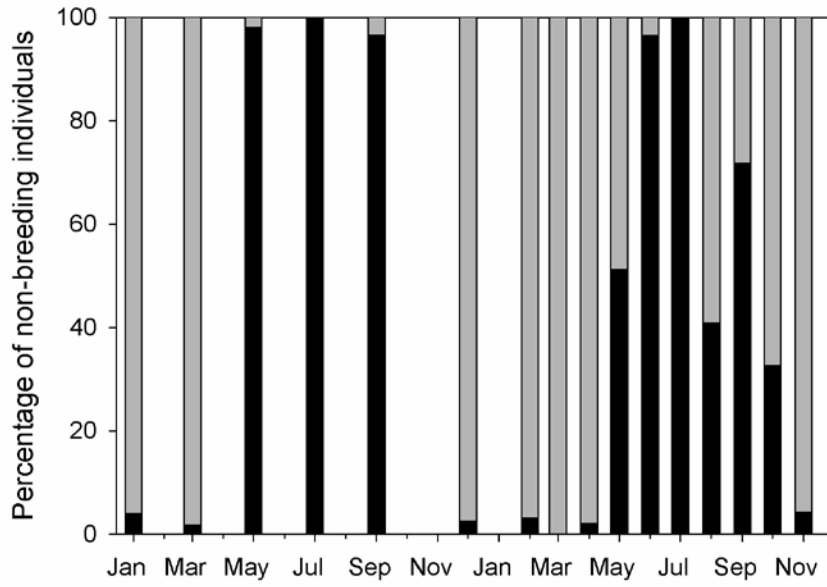
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569 **Figure 3:** The seasonal changes in the percentage of non-breeding mute swans in the River Frome catchment

570 using river (black bars) and pasture (grey bars) habitat. After Wood (2012).

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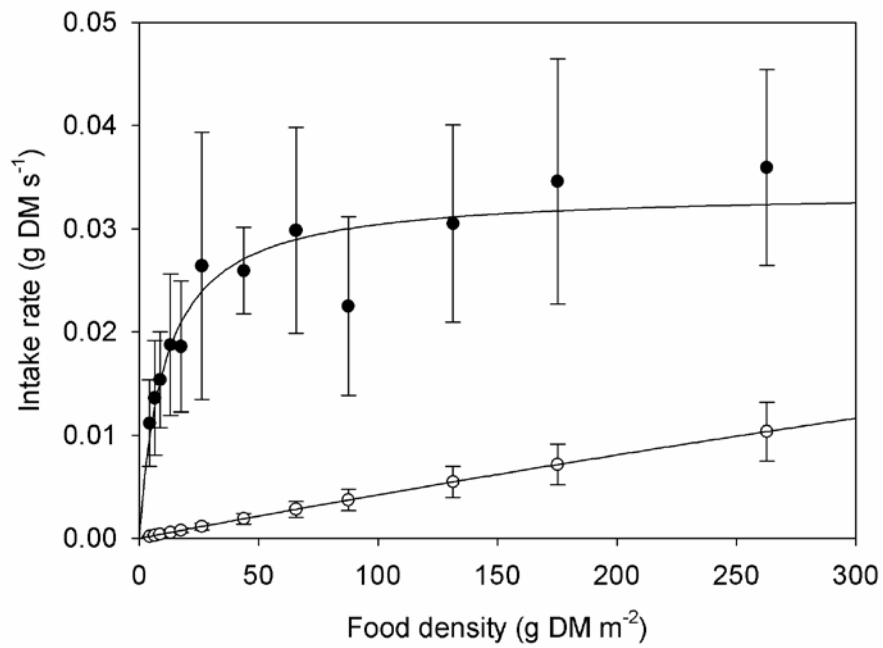
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589 **Figure 4:** The mean (\pm 95 % CI) mute swan intake rates when feeding on water crowfoot (solid markers) and

590 pasture grass (open markers).

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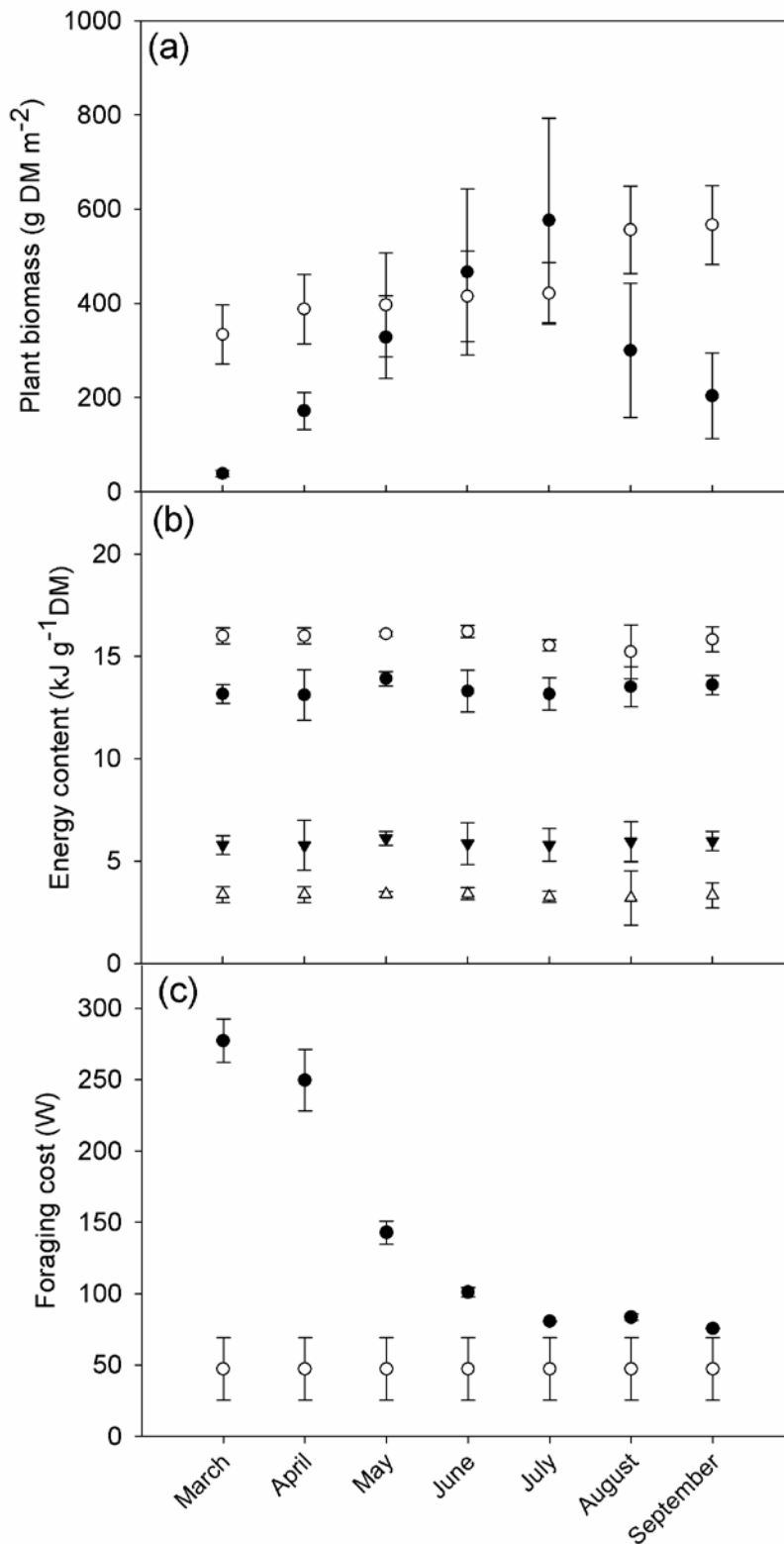
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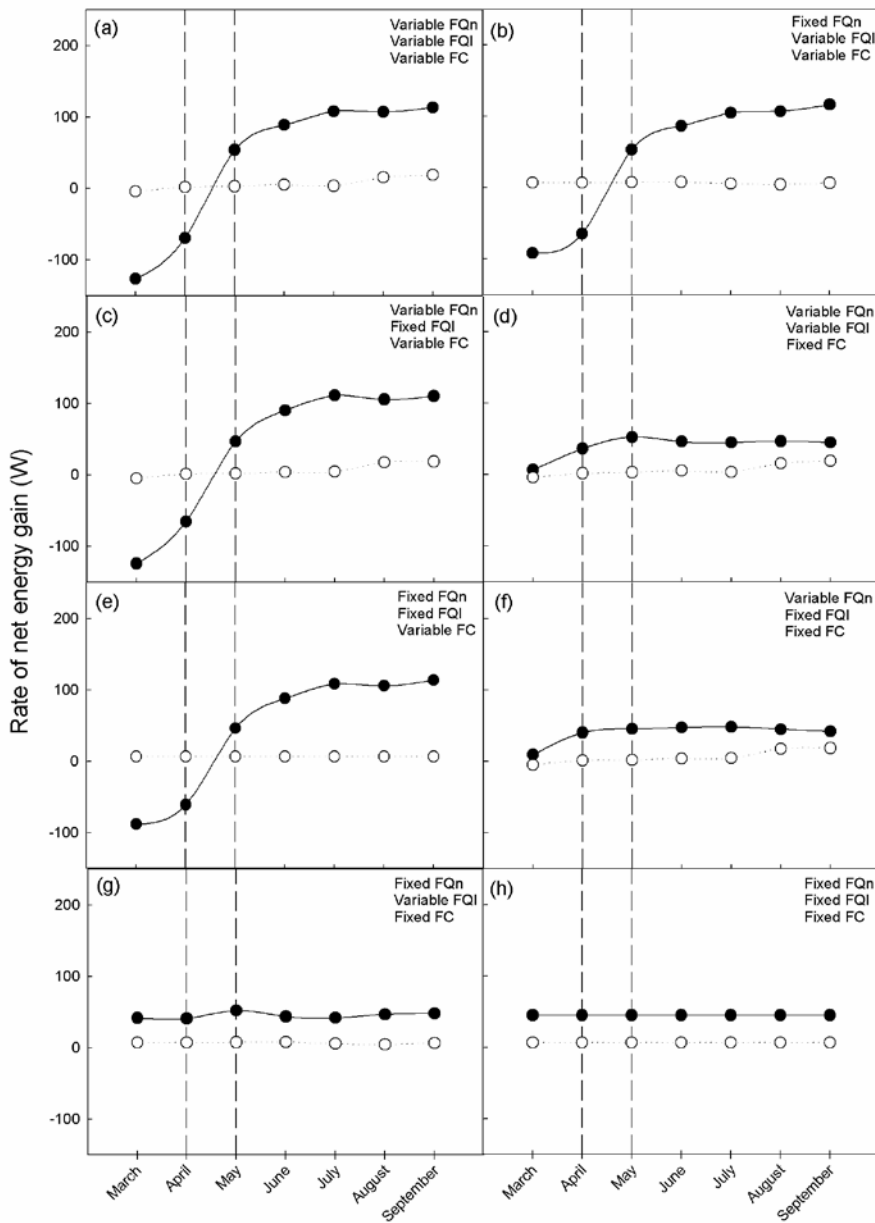
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607 **Figure 5:** Monthly changes for water crowfoot (solid markers) and pasture grass (open markers) in terms of
 608 mean \pm 95 % CI (a) biomass g DM m⁻², (b) gross (circles) and metabolisable (triangles) energy content, and (c)
 609 foraging costs.



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Figure 6: The changes in swan foraging profitability (rate of net energy gain in W) for water crowfoot (solid circles) and pasture grass (open circles) predicted by our foraging models (a-h). The observed diet and habitat switch occurred between April and May, indicated by the dashed lines.

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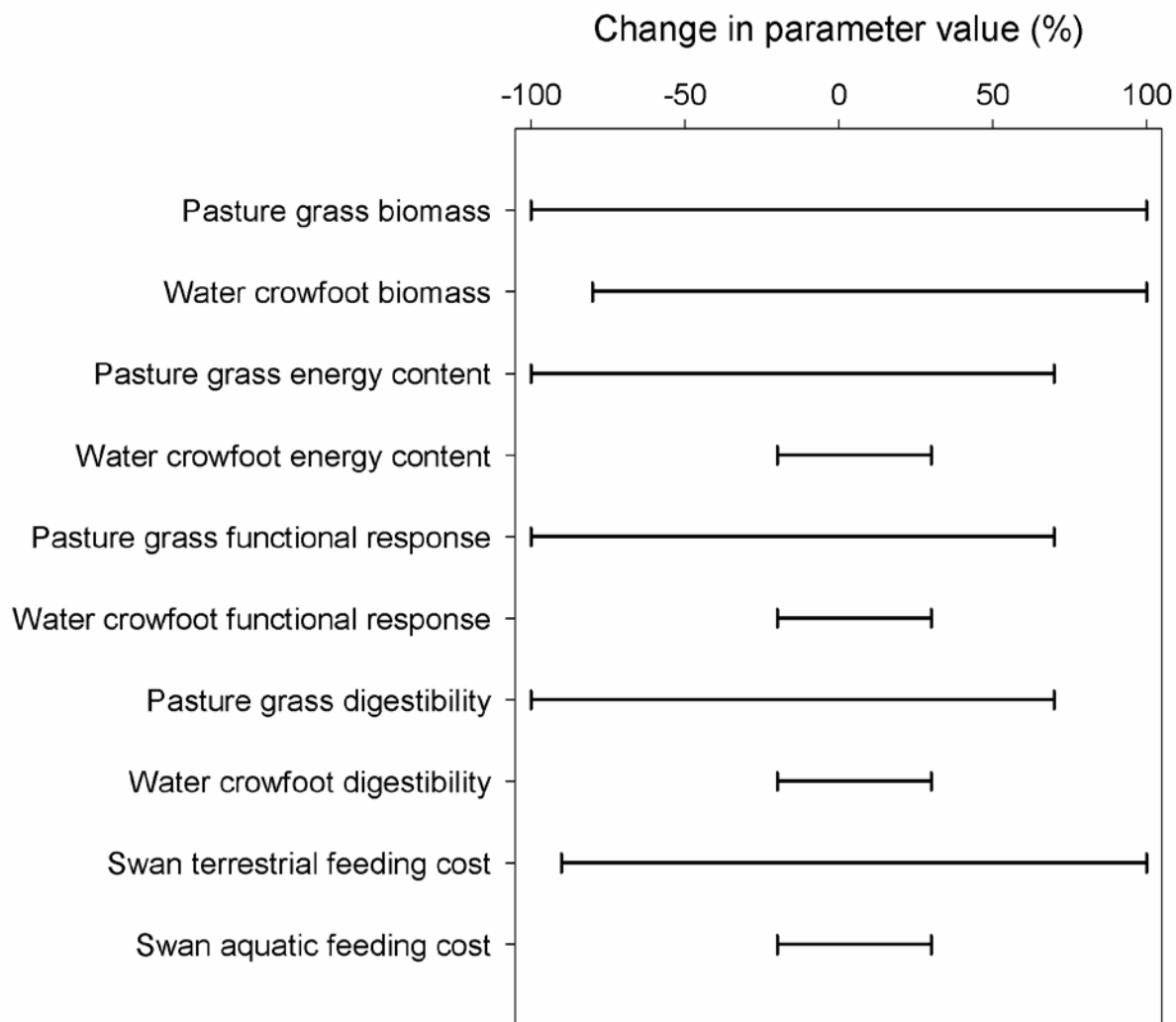
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622 **Figure 7:** The relative sensitivity of our model to changes in the value of each parameter, indicating the range of

623 values within which our model predictions are likely to be robust. We sequentially decreased and increased

624 values in 10 % increments within the range -100 % to 100% of the original value. From this process we

625 recorded the values at which the model no longer yielded accurate predictions of the habitat switch date.

626