

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

Kevin A. Wood, Richard A. Stillman, Dave Wheeler, Steve Groves, Catherine Hambly, John R. Speakman, Francis Daunt and Matthew T. O'Hare

K. A. Wood (*kevinwoodecology@hotmail.co.uk*), F. Daunt and M. T. O'Hare, *Centre for Ecology and Hydrology, Edinburgh, Midlothian, EH26 0QB, UK.* – KAW and R. A. Stillman, *School of Applied Sciences, Bournemouth Univ., Poole, Dorset, BH12 5BB, UK.* – D. Wheeler and S. Groves, *Abbotsbury Swannery, New Barn Road, Abbotsbury, Weymouth, Dorset, DT3 4JG, UK.* – C. Hambly and J. R. Speakman, *Inst. of Biological and Environmental Sciences, Univ. of Aberdeen, Aberdeen, AB24 2TZ, UK.* JRS also at: *State Key Laboratory of Molecular and Developmental Biology, Inst. of Genetics and Developmental Biology, Chinese Academy of Sciences, 1 West Beichen Road, Chaoyang, CN-100101 Beijing, PR China.*

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

Explaining the spatiotemporal patterns of animal diet and distribution is a central challenge facing ecologists. The most common explanation holds that foragers should attempt to select the habitat and diet that allow them to maximise their intake rate of energy and nutrients over time whilst minimising metabolic foraging costs and risk of exposure to harmful stimuli (e.g. toxins) and predation (Stephens and Krebs 1986, Newman et al. 1995, Killen et al. 2007). The most profitable food resource is that which yields the greatest net energy gain (gain minus cost). The predictions of optimal diet theory have been upheld in a range of different field tests (Owen-Smith and Novellie 1982, Nolet et al. 2001, Babin et al. 2011). The theory has proven particularly robust for animals which feed on immobile prey, such as herbivores consuming plant tissues (Sih and Christensen 2001). Three key factors can determine what the most profitable diet should be, and consequently where the animals should feed; food quantity, food quality and foraging costs (Stephens and Krebs 1986). Increases in both the quantity and nutritional quality will increase the profitability of a food resource,

making it more attractive to foragers (Owen 1972, Owen-Smith and Novellie 1982, Illius et al. 1999). In contrast, increased foraging costs lower the profitability of a food resource. Foraging costs may be direct costs such as the energy expenditure required to search for, capture and consume a prey item, or indirect costs such as increased predation risk (Stephens and Krebs 1986).

Optimal foraging models, which calculate the relative gains and costs associated with different available diets and habitats, have proven to be a useful tool to successfully predict forager diet and habitat choice (Owen-Smith and Novellie 1982, Newman et al. 1995, Inger et al. 2006). However, to yield accurate predictions such models require accurate data on the food quantity, food quality and foraging costs that foragers face (Wilson et al. 2012). Many models use fixed values of food quantity, food quality and foraging costs, and thus neglect temporal variance in such parameters. Previous studies have examined the effects of seasonal variance in the quantity and quality of different food resources on animal foraging decisions (Prins and Ydenberg 1985, Vickery et al.

1995, Nolet et al. 2001). However, few studies to date have demonstrated a habitat shift caused by seasonal changes in metabolic foraging costs. Indeed, most studies assume that the metabolic costs of foraging on a given food resource are fixed over time. This is despite the potential for large seasonal variations in metabolic foraging costs between different habitats. There are many species which switch between different foraging habitats, such as those that switch between aquatic and terrestrial habitats, lentic and lotic habitats, or aerial and ground habitats (Prange and Schmidt-Nielsen 1970, Sherer and Wunder 1979, Clausen et al. 2012). Therefore studies are needed to explore the influence of seasonal changes in food quantity, food quality and foraging costs on the behavioural decisions of foraging animals.

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

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

Methods

Study system

Our study system was a mesotrophic chalk river catchment, the River Frome (Dorset, UK), from Maiden Newton

(50°46'N, 02°34'W) 44 km downstream to West Holme (50°41'N, 02°10'W). The main river channel is dominated by the aquatic plant stream water crowfoot *Ranunculus penicillatus* ssp. *pseudofluitans* (Wood et al. 2012a). The river is typically bordered by terrestrial pasture fields dominated by perennial ryegrass *Lolium perenne*, creeping bentgrass *Agrostis stolonifera* and Yorkshire fog *Holcus lanatus*, which frequently become water-logged during winter (Wood et al. 2013a). Predation risk for adult swans is very low and does not differ between habitat types (<3% of all mortality; Brown et al. 1992).

Food quality

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

We measured the nutritional quality of water crowfoot and pasture grass, in terms of energy content, at four of our sites each month between March and September. Randomly selected samples (n = 3) from four river and four adjacent field sites were ground for 300 s at 25 Hz in a ball-mill. This sub-sampling approach was used as it was not economically viable to analyse samples from all sites; these four sites were selected as they were characteristic of the catchment in terms of land use, sediment composition and plant community. Prior to analyses samples were redried at 105°C for 3 h in an oven. To determine energy (kJ g⁻¹) content 0.20 ± 0.01 g DM of each sample was analysed using a semi-micro oxygen bomb and oxygen bomb calorimeter.

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

$$ME = GEI - FEO/GMI$$

where *ME* was the plant metabolizable energy content (kJ g⁻¹ DM), *GEI* was the swan daily gross energy intake (kJ), *FEO* was the swan daily faecal energy output (kJ) and *GMI* was the swan gross dry matter intake (g). Swan *GMI* was calculated as the product of swan daily foraging time (*FT*) and swan intake rate for that plant species. *FT* was estimated at 27562 s (31.9% of day) and 49766 s (57.6% of day) when feeding on water crowfoot and pasture grass respectively, based on the time budget study reported in Wood (2012). For water crowfoot we assumed an intake rate of 0.032 g DM s⁻¹ based on the functional response for biomass and

gross energy content values of 297.8 g DM m⁻² and 13.4 kJ g⁻¹ DM respectively. For pasture grass we assumed an intake rate of 0.016 g DM s⁻¹ based on the functional response for biomass and gross energy content values of 439.7 g DM m⁻² and 15.8 kJ g⁻¹ DM respectively. *GEI* for swans feeding on each plant species was estimated as the product of *GMI* and gross energy content for that species. We calculated as *FEO* as:

$$FEO = ((FT \times FR) FM) FE$$

where *FT* was daily foraging time (s), *FR* was the rate of excretion whilst foraging (droppings s⁻¹), *FM* was mass per dropping (g), and *FE* was the energy content per dropping (kJ g⁻¹ DM). *FR* was estimated from the allometric equation for waterfowl provided by Hahn et al. (2008): $\log_{10} FM = 10^{2.130} \times M^{-0.3065}$, which we converted to droppings per second. *M* was species body mass (10 800 g; Kear 2005). Mean \pm 95 % CI values for *FM* were estimated at 8.5 \pm 3.3 and 7.4 \pm 1.9 g DM dropping⁻¹ for water crowfoot and pasture grass respectively, based on measurements of 40 faecal samples (20 water crowfoot and 20 pasture grass) collected over the study period, dried and weighed according to the protocol for plant samples. *FE* was estimated using the bomb calorimetry protocol as for plant samples, which gave mean \pm 95% CI values for water crowfoot of 9.96 \pm 1.38 kJ g⁻¹ DM (n = 9) and for pasture grass of 12.90 \pm 1.00 kJ g⁻¹ DM (n = 9). Thus we calculated *FEO* for water crowfoot foraging as 6573 kJ and for pasture grass foraging as 7175 kJ.

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

$$\text{metabolizability} = (ME/GE) 100$$

where *ME* was the plant metabolizable energy content (kJ g⁻¹ DM) and *GE* was the plant gross energy content (kJ g⁻¹ DM). Thus metabolizability for water crowfoot was 44% and for pasture grass was 21%.

Food quantity

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

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

where *H* was the sward height in cm, and *a* and *b* were the bite size and handling time (3.6 and 0.02 respectively) derived by van Gils et al. (2007). We modified this equation

so that intake rate was expressed for a given pasture grass biomass (*B*, in g DM m⁻²) rather than sward height (*H*, in cm); using the sward height and biomass data from our 18 field sites. We found a significant, positive relationship between mean sward height and biomass for all months at all sites (linear regression: $F_{1,124} = 211.9$, $p < 0.0001$, $R^2_{adj} = 63\%$). Thus we converted sward height to sward biomass according to the following relationship:

$$H = 0.0238 \times B$$

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

$$\log_{10} I = -4.89 + 0.81 \log M$$

where *M* = mean species body mass (g). We used this equation to calculate the relative difference between the pasture grass intake rates of Bewick's (0.0148 g DM s⁻¹) and mute (0.0238 g DM s⁻¹) swans, assuming body mass values of 6000 g and 10 800 g respectively (Kear 2005). We calculated the intake rate of a mute swan relative to a Bewick's swan as:

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

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

$$I_{Mute} = I_{Bew} \times 1.61$$

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

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

$$\text{consumption} = R_b - (R_a + R_w)$$

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

Foraging costs

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

$$\text{BMR} = (VO_2 \times m) e$$

where VO_2 was the consumption of oxygen (ml O₂ g⁻¹ s⁻¹) as reported in Bech (1980), m was mean swan mass (10 800 g) as given in Kear (2005), and e was the energy yielded per ml of oxygen consumed (kJ ml⁻¹ O₂) assuming a conversion of 0.02 kJ ml⁻¹ O₂ (Nolet et al. 2002). Thus we estimated mute swan BMR as 39 W. We calculated the energetic cost of terrestrial foraging as the multiple of basal metabolic rate (BMR) reported for a congenial species, the Bewick's swan, in Nolet et al. (2002), yielding a mean ± 95% CI value of 47 ± 22 W. Whilst BMR increases with mean body mass across species, the metabolic costs of behaviours as a multiple of BMR are consistent between closely related, morphologically-similar species such as mute and Bewick's swans (Bruinzeel et al. 1997). To estimate the energetic cost of aquatic foraging, we calculated the cost of swimming at a given water velocity (v ; m s⁻¹) using the mean relationship between the multiple of BMR (\times BMR) and standardised swimming speed L (body lengths^{0.4} s⁻¹; Ware 1978) for barnacle geese *Branta leucopsis* (Nolet et al. 1992), northern mallard *Anas platyrhynchos* (Prange and Schmidt-Nielsen 1970) and tufted duck *Aythya fuligula* (Woakes and Butler 1986), as such data for swans were unavailable (Fig. 1):

$$\times\text{BMR} = 1.5 + (-1.2L) + 2.4(L^2)$$

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

$$FC = (\times\text{BMR}_v \times \text{BMR}) + TC$$

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

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

As mute swans and northern mallards are closely related (Order: Anseriformes) they have a highly similar morphology and swimming action. Furthermore, as functionally similar surface-swimming birds both species have the same hull

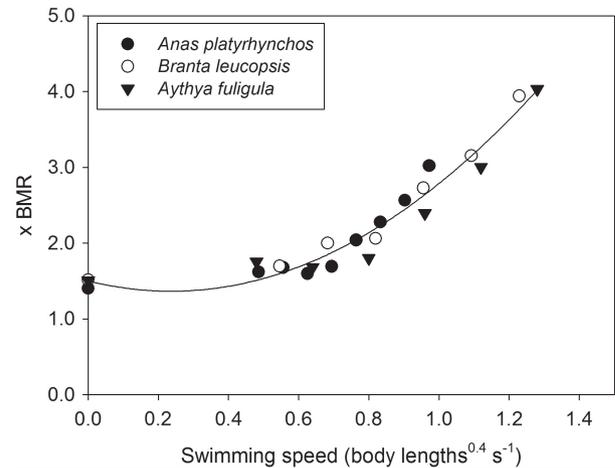


Figure 1. The relationship between swimming speed and the energetic cost of swimming, expressed as the multiple of BMR, based on three published studies.

design, a displacement hull, which determines the shape of the relationship between energy expenditure and water velocity (Prange and Schmidt-Nielsen 1970). Therefore we expected an equivalent BMR-swimming speed relationship for both species. Daily mean water discharge (m³ s⁻¹) measurements between 1 March and 31 September 2010 were provided by the Environment Agency for the East Stoke gauging station (station number 44001; 50°41'N, 02°11'W), from which daily mean water velocity (m s⁻¹) values were calculated for this period (Fig. 2). Because water discharge, velocity and channel cross sectional area (width multiplied by depth) are interrelated according to the relationship, discharge = velocity × cross sectional area, we carried out a back calculation of velocity that was based on the standard technique used to derive depth–discharge relationships for gauging station rating curves, although in this instance velocity, not depth was derived (Bovee and Milhouse 1978, Gordon 1992). River cross sections were available for East Stoke, recorded using the methods described in Wood et al. (2012c). Only four cross sectional areas were available and hence some caution was necessary in interpreting the results, however it is known that three points are sufficient to extrapolate within the range 40–250% of calibrated flow (Bovee

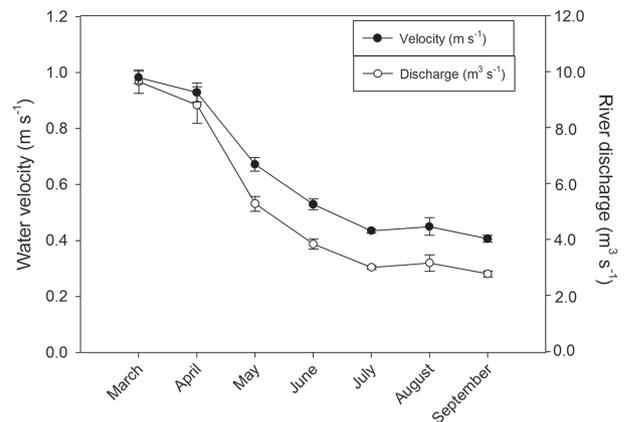


Figure 2. Monthly changes in mean ± 95% CI gauged discharge and calculated velocity for the study area.

and Milhouse 1978). Mean cross sectional velocity (v , in m s^{-1}) was calculated according to the formula:

$$v = a (1 - \exp(-b \times Q))$$

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

We assumed that BMR did not vary with temperature for terrestrial foraging as Bech (1980) demonstrated that mute swans are thermoneutral in air between 1 and 15°C , which corresponds with the temperature range within our study system (Wood et al. 2012a). However, animals typically incur an additional thermoregulatory cost when in water compared with terrestrial activity. Jenssen et al. (1989) found that, $< 15^\circ \text{C}$, the additional thermoregulatory cost (TC ; W kg^{-1}) to surface-swimming waterfowl varied with temperature according to the equation:

$$TC = 1.80 - (0.09 \times t)$$

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

Foraging models

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

$$\text{profitability} = ((FQI \times d) I_{FQn}) - FC$$

where FQI was the gross energy content ($\text{kJ g}^{-1} \text{DM}$), d was the digestibility as a proportion of the gross energy 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 metabolic cost of foraging (kJ s^{-1}).

We sequentially tested all eight combinations of models of fixed and variable values for food quantity (FQn ; g DM m^{-2}), food quality (FQI ; $\text{kJ g}^{-1} \text{DM}$) and foraging costs (FC ; kJ s^{-1}). Where parameters were variable, the

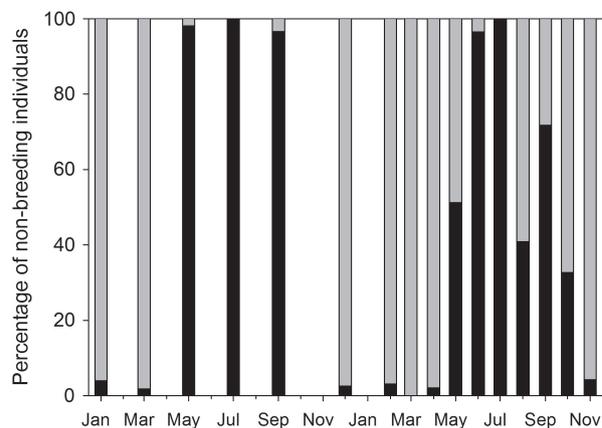


Figure 3. The seasonal changes in the percentage of non-breeding mute swans in the River Frome catchment using river (black bars) and pasture (grey bars) habitat. After Wood et al. (2013a).

mean value for each month was used. Where parameters were fixed, the mean value for the March to September was used. This approach allowed us to examine how the profitability of the two food resources changed under conditions of fixed or variable food quantity, food quality and foraging costs, and assess how such changes affected the food resource swans were predicted to exploit. The 'best' model was the one which required the fewest parameters to successfully predict that the observed habitat switch would occur between April and May (Fig. 3; Wood et al. 2013a), as this model was the most parsimonious in terms of data required.

Sensitivity analysis

To quantify how sensitive our best model predictions were we performed a sensitivity analysis following the one-at-a-time method of local sensitivity analysis. For each parameter in our best model we 1) increased the value in 10% increments from 0% to 100% and 2) decreased the value in 10% increments from 0 to 100%; the percentage increase and decrease at which the model no longer correctly predicted the habitat switch date. This process yielded for each parameter the range of values within which our model predictions are likely to be robust.

Results

Food quality

Limited between-month variance was found in the mean ($\pm 95\%$ CI) gross energy content of water crowfoot ($13.4 \pm 0.2 \text{ kJ g}^{-1} \text{DM}$) and pasture grass ($15.8 \pm 0.3 \text{ kJ g}^{-1} \text{DM}$) (Fig. 5b). No consistent seasonal trend in energy content was observed for either plant.

Food quantity

When foraging on water crowfoot swan intake rate (I , in g DM s^{-1}) increased with food density (B , in g DM m^{-2}) according to the relationship $I = (0.0031 (\pm 0.0006) B) / (1 + (0.0934 (\pm 0.0207) B))$ (Fig. 4). Water crowfoot

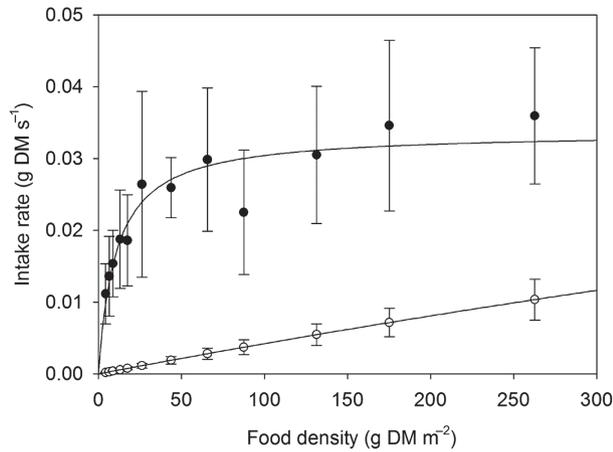


Figure 4. The mean (\pm 95% CI) mute swan intake rates when feeding on water crowfoot (solid markers) and pasture grass (open markers). Intake rate for water crowfoot was estimated from experimental feeding trials, whilst the intake rate for pasture grass was estimated from an allometric scaling relationship between pasture grass biomass and waterfowl intake rates.

biomass exhibited a strong seasonal pattern, increasing from 38.5 g DM m⁻² in March to a seasonal maximum of 576.4 g DM m⁻² in July, declining thereafter (Fig. 5a). Pasture grass biomass showed a gradual 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 September (Fig. 5a). Mean biomass values for the March to September period were 297.8 g DM m⁻² and 439.7 g DM m⁻² for water crowfoot and pasture grass respectively.

Foraging costs

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 September (Fig. 2). Accordingly, the cost of aquatic foraging declined over the study period from 277 W in March to 75 W in July (Fig. 5c). The additional thermoregulatory cost of aquatic foraging accounted for a mean of just 2.7% (range 0.0 to 8.6%) of the total metabolic cost of aquatic foraging. Additionally, as mean water temperature exceeded the 15.0°C threshold in June (16.9°C), July (18.0°C), and August (15.7°C), the additional thermoregulatory cost of aquatic foraging was 0 W in these months. The mean foraging cost between March and September was 144 W. However, in all months the cost of aquatic foraging was higher than the cost of terrestrial foraging. The cost of terrestrial foraging was assumed not to vary (47 W).

Foraging models

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

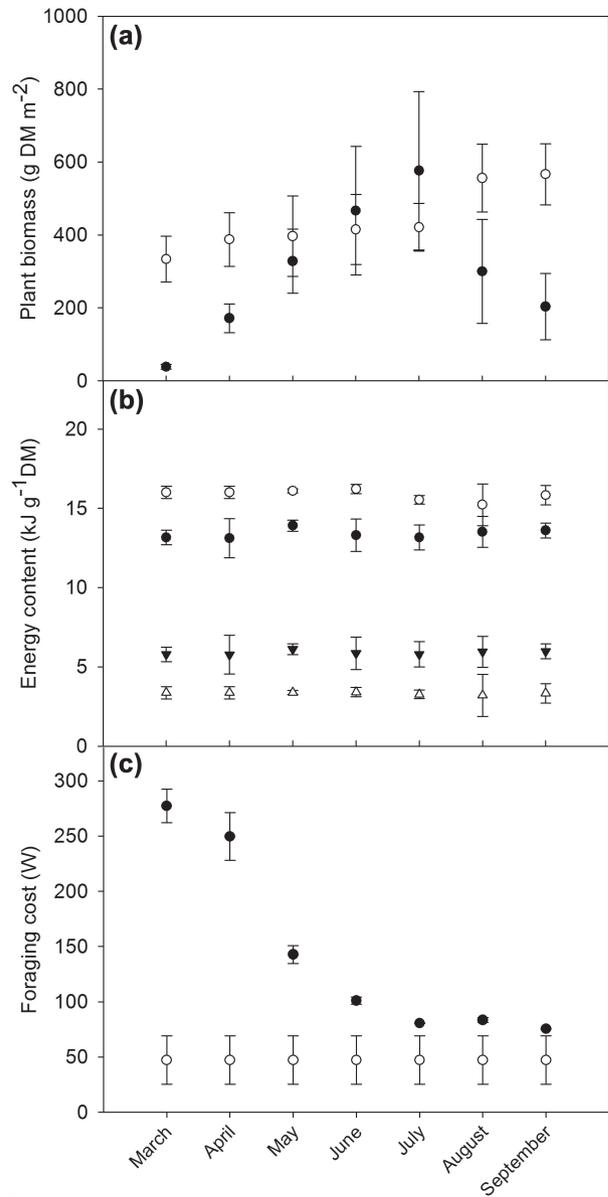


Figure 5. Monthly changes for water crowfoot (solid markers) and pasture grass (open markers) in terms of mean \pm 95% CI (a) biomass g DM m⁻², (b) gross (circles) and metabolisable (triangles) energy content, and (c) foraging costs.

Sensitivity analysis

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

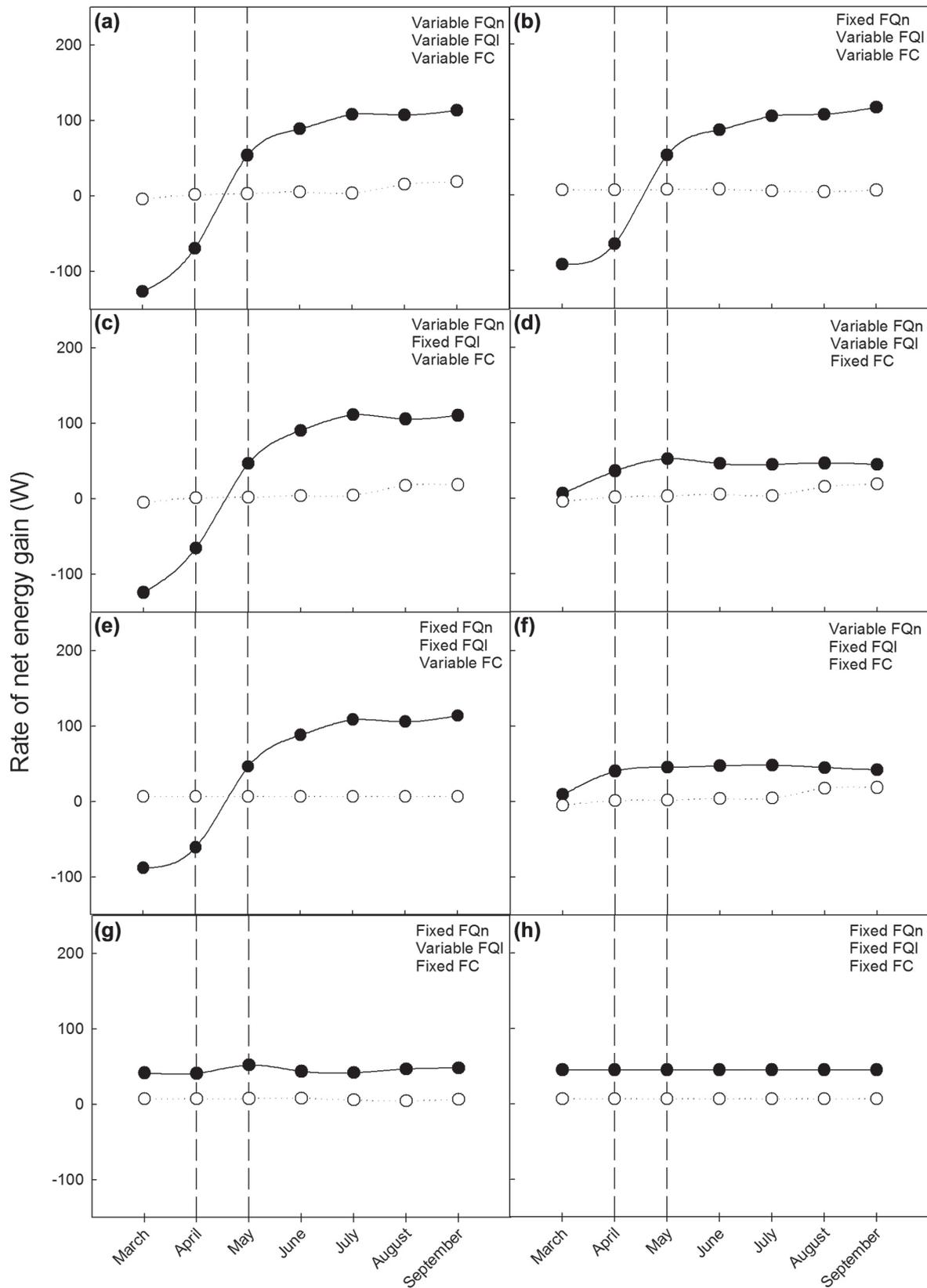


Figure 6. We used an optimal foraging model to predict the date of the observed shift of non-breeding mute swans from terrestrial to aquatic habitat. The changes in swan foraging profitability (rate of net energy gain in W) for water crowfoot (solid circles) and pasture grass (open circles) were predicted by our foraging models (a–h) based on seasonally varying (variable) or seasonal mean (fixed) values for food quantity (FQn), food quality (FQI), and foraging cost (FC). The observed diet and habitat switch occurred between April and May, indicated by the dashed lines.

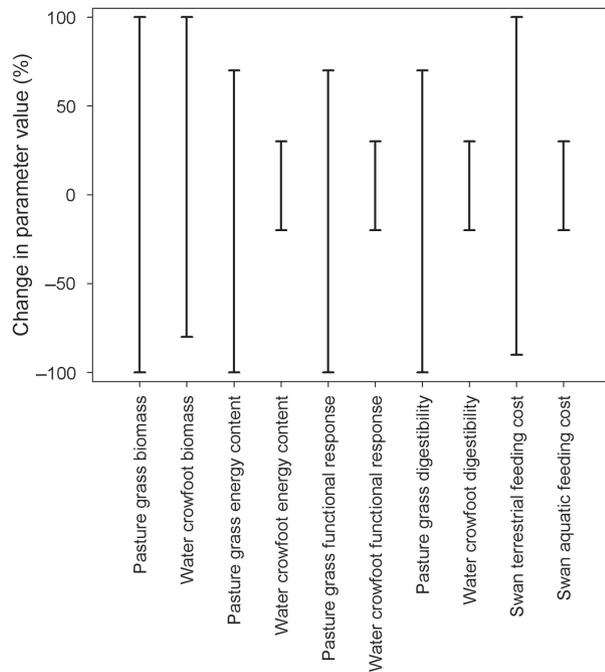


Figure 7. The relative sensitivity of our model to changes in the value of each parameter, indicating the range of values within which our model will correctly predict the observed habitat switching date. We sequentially decreased and increased values in 10% increments within the range -100% to 100% of the original value. From this process we recorded the values at which the model no longer yielded accurate predictions of the habitat switch date.

values (Fig. 6d, f, g); in particular, no magnitude of change in any parameter caused a correct prediction (i.e. April–May habitat switch) to be made.

Discussion

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

To accurately predict the date when swans would switch from terrestrial to aquatic foraging, we needed to include seasonal variance in foraging costs in our model. However, we did not need to include seasonal variance in food quantity and food quality, as accurate predictions could be obtained with fixed values for these two parameters. Food quantity in the river increased more steeply than in pasture fields between March and July and therefore could have potentially explained the observed habitat shift; however, the models suggested that these changes in food quantity alone did not affect the relative profitability of the two food resources. The swan functional response to water crowfoot biomass could at least partially explain this; as water crowfoot biomass ranged between $40\text{--}580\text{ g DM m}^{-2}$ (Fig. 5a),

our functional response curve suggests almost no increase in intake rate over this range. Hence swan intake rate on water crowfoot was almost invariant over the seasonal range of biomass values. Although our study was correlational, the results suggested that the seasonal changes in foraging costs may have been a key factor influencing the decision of the swans to switch feeding habitats, supporting our third hypothesis (H3). These seasonal changes in foraging costs appeared to be related to changes in water velocity; the profitability of aquatic foraging was negatively related to water velocity, as faster water required more energy to be expended swimming (Prange and Schmidt-Nielsen 1970, Butler 2000, Bejan and Marden 2006). For this same reason, the costs of non-foraging activities would also be higher in the river compared with the terrestrial habitat. Therefore swans appear to delay switching to the river until the net rate of energy gain whilst foraging compensates for the additional metabolic cost of activities in flowing waters. We did not have the data to examine the reverse shift from river to pasture that has been observed between October and November (Wood et al. 2013b). However, water velocity is known to increase in response to the seasonal increase in precipitation which occurs during this period, which suggests that changes in water velocity may again drive this swan habitat shift later in the year (Wood et al. 2013a). In contrast to some other animals, such as ungulates (Beier and McCullough 1990), inter-habitat differences in temperature and associated thermoregulatory costs had little effect on swan habitat use. Waterfowl have low thermal conductivity due to their dense plumage, which results in low additional thermoregulatory costs for aquatic feeding in temperate regions (Jenssen et al. 1989, van Sanst and Bakken 2006). However, at higher latitudes additional thermoregulatory costs can be much greater due to substantially lower temperatures (Irving et al. 1955, Lefebvre and Raveling 1967).

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

Knowledge of the energy gains and costs between different habitats permits the construction of energy landscape (sensu Wilson et al. 2012); models which incorporate the spatial variation in energy gains and costs can yield a mechanistic, process-based understanding of decision making in animals, such as habitat selection. If the factors which

control animal movements can be understood, such factors might be manipulated to influence the distribution of animals within the landscape. Mechanistic models which can make accurate, robust predictions regarding animal habitat selection and energy balance could therefore be useful tools for wildlife managers. Scenarios where the management of animal distributions may be required include species of conservation concern, species where harvestable populations are desired (e.g. shooting quarry), and pests of agriculture (Sutherland 1998, Gordon et al. 2004, Wood et al. 2013b). In this way the insights of behavioural ecology could be used to inform wildlife management.

Our study indicates the importance of comparing values of profitability for food resources in different habitats, with different associated costs, within a landscape. Crucially, where inter-habitat differences in metabolic foraging costs exist, such comparisons must include estimates of the energetic costs of foraging on each food resource, not just the gross gains. Highly mobile foragers such as waterfowl can track the most profitable food resource as seasonal changes in foraging costs occur. Our results demonstrate that, at least where strong seasonal changes in foraging costs occur, these changes should be included in calculations of the profitability of different food resources available to foragers to allow the construction of an energy landscape.

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