

Behavioural adaption of Scaly-sided Merganser (*Mergus squamatus*) to habitats with different water depth: different activity profile but the same foraging energetics

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Abstract

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Keywords : Foraging behaviours adaption; Foraging energetics; In-stream habitats; Morphological specialization.

1. Introduction

Wild animals have been constantly subjected to environmental fluctuations during their evolutionary history, and have evolved to match physiology and behaviour to the predictable environmental variations in their natural habitats (Schmidt-Nielsen, 1997). Adjusting behaviour is often the first response when environmental conditions are altered (Snell-Rood, 2013). Behavioural responses are not always adaptive, but the ability of wildlife to behave appropriately in response to environmental changes is crucial for their survival (Sih, Ferrari, & Harris, 2011; Wong & Candolin, 2015). Behavioural plasticity could allow species to adjust behaviour to suit the conditions of its immediate environment and, in so doing, increase its fitness (Van Buskirk, Candolin, & Wong, 2012).

Among all adaptive tactics, foraging behaviours are most advantageous and allow the species to navigate diverse landscapes while efficiently searching for food (Schoener, 1971), and gain physiological, survivorship, and fitness benefits (Hadfield & Strathmann, 1996). For example, Great knots (*Calidris tenuirostris*) extended their feeding time and adjusted their food selection to adapt the suddenly decline of original main food (Zhang et al., 2019).

Some young salmonid fishes clearly decrease their foraging behaviours from still water habitats to slow-running waters to fast-running waters (Tunney & Steingrímsson, 2012). To assess animals' foraging plasticity

in a changing environment, habitat–behaviour interactions within the wide array of environmental conditions are to be characterized (Gilmour et al., 2018).

Flexible and specialized foraging strategies are dependent on the stability of available resources in habitats (West-Eberhard, 1989). For most waterbirds, water depth might be the primary of habitat quality (Zeng, Lu, et al., 2018). Different water depths mean different species, sizes and quantities of food and therefore a key factor to affect their foraging behaviours and techniques (Giraldo et al., 2017; Harvey & Stewart, 1991).

Scaly-sided Merganser (*Mergus squamatus*) is endemic to east Asia and is listed as globally endangered (BirdLife & International, 2017). It's a habitat specialist, which occurs on clear, flowing rivers in the mountainous regions (Zeng, Wei, & Lei, 2018). It mainly breeds in southeastern Russia, and northeast China, and winters in the central and southern China, especially middle and lower Yangtze River (Zeng, Wei, et al., 2018; Zhao & Pao, 1998). *M. squamatus* is an opportunist piscivore who selects the most abundant food source (Zhao & Pao, 1998), such as fish and macroinvertebrates. It has long thin hooked bill with many serrations at the tip (Zhao & Pao, 1998) and is adapted to active hunting of moving prey in water column. *M. squamatus* mainly takes two foraging modes: diving and head-dipping (Solovieva, 2013; Zhao & Pao, 1998). In breeding areas, *M. squamatus* usually immerses its head into shallow waters to pick aquatic insects and use diving techniques to catch fish in deep waters (Solovieva, 2013; Zhao & Pao, 1998). Foraging strategy and energy budgets of *M. squamatus* were unknown in the wintering grounds (Solovieva, 2013).

The loss of lateral and longitudinal connectivity of free-flowing rivers through flow regulations such as damming presents a major threat to global freshwater biodiversity (Barbarossa et al., 2020; Dudgeon, 2019; Tonkin, Heino, & Altermatt, 2018) including the obligated freshwater megafauna (He et al., 2019) and foragers such as waterbirds (Zeng, Lu, et al., 2018). Knowledge of animal behaviour is fundamental in understanding and mitigating the effects of habitat loss and fragmentation. In this study, using three years (from 2018 to 2020) of video footages of *M. squamatus* foraging at the wintering habitats with different water depths, we aim to evaluate the extent to which foraging behaviour flexibility and plasticity exist. We also compare the foraging energetics in different habitats by estimating the behavior energy costs, fish catch rates, and energy intakes. We use these findings to highlight the risk of the rapid anthropogenic environmental changes to habitat specialists (Sih et al., 2011).

2. Material and Methods

2.1 Study area

This study was conducted in a 5 km reach of the Shangqing River in Jiangxi province (Fig. 1), a tributary of Yangtze River. The site is a major *M. squamatus* wintering ground, providing foraging habitat for a population of about 50 individuals every year (Wang et al., 2010). The average annual temperature is 16.7 and the average annual precipitation is 1816 mm. Both sides of the river were covered by forest. There are many gravel bars and islands in this river reach, providing ideal habitats for *M. squamatus* to forage and roost ((Zeng et al., 2015)). The water depth varies from 0 to 3 meters. Considering the different foraging behaviours, we classified areas with water depth up to 40 cm as shallow and those greater than 40 cm as deep (Fig. 1).

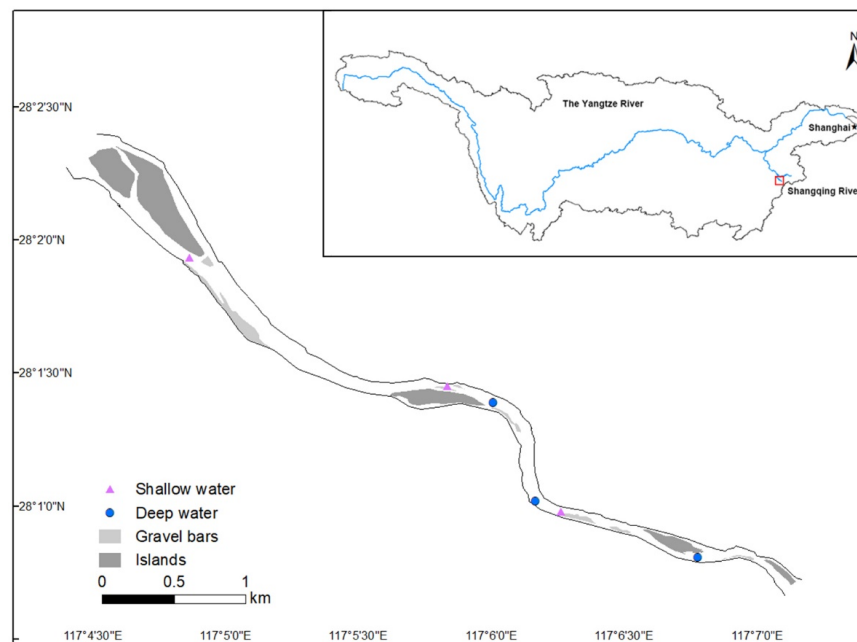


Figure 1. The study area in Shangqing River and its location in the Yangtze River basin

2.2 Behaviour recordings and identification

Video recording was often used to monitor the foraging behaviour in a natural complex environment (Bruijn, Vosteen, Vet, Smid, & Boer, 2021). In this study, video footages (Nikon P900S) were taken from six fixed locations (3 for each habitat types, Fig. 1) to record the foraging activities of *M. squamatus* in three winters (2018-2020). Recording was initiated when a bird started a foraging bout (see below) and the camera then followed the bird till it finished the foraging or disappeared from the range of view. Based on field observation and examining the videos, we defined the duration of a foraging bout as the time interval encompassing the descending, swimming, diving, and the subsequent resting on the water surface and taking off (Table 1). Each foraging bout could last for 3-15 minutes and contained multiple activities.

We focused on the foraging behaviours of individuals, which were identified as 8 activities from 3 related types: fishing, preparing and other social activities (Table 1). Here we distinguished two main fishing behaviours: diving and head-dipping (Fig. 2). While diving is mainly performed in deep waters, head-dipping is the main fishing tactic in shallow waters. The length of time that a *M. squamatus* spent in each behaviour was divided by the length of the foraging bout to give the percent of time spent in each behaviour.

Table 1. Description of identified behaviours of Scaly-sided Merganser

M. squamatus

No.	Type	Behaviour	Description
1	Fishing	Eye-submerging	Submerging eyes into water
2		Head-dipping	Submerging head under surface water
3		Diving	Diving under surface water
4	Preparing	Food handling	Handling fish on the water surface
5		Vigilance	Looking around to detect and avoid threats of predation and intraspecific competition
6		Swimming	Swimming on the surface of the water
7		Preening	Any maintenance done to feathers, including straightening and oiling feathers

No.	Type	Behaviour	Description
8	Others	Social interacting	Intraspecific interaction and interspecific interaction

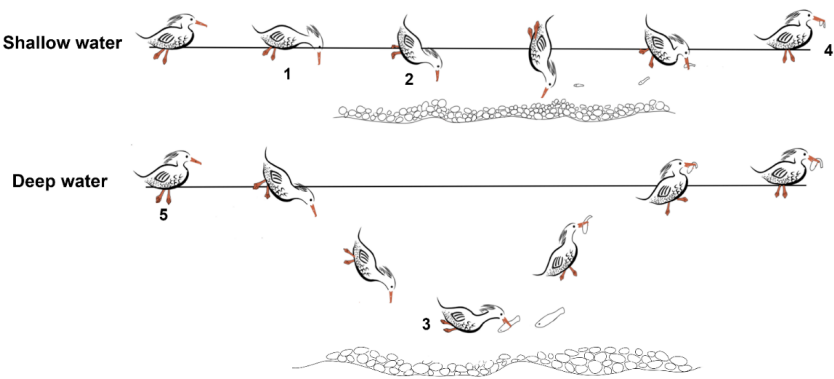


Figure 2. The identified foraging behaviours of *M. squamatus* at different water depth

2.3 Video analysis

All videos were analyzed in Boris Video v7.9.1. BORIS (Behavioural Observation Research Interactive Software, University of Torino) is a free, open-source and multiplatform standalone program that allows a user-specific coding environment to be set for a computer-based review of previously recorded videos or live observations (Friard & Gamba, 2016). The software has been used in study behaviour of human, farm animals, and wildlife (Aletta, Lepore, Kostara-Konstantinou, Kang, & Astolfi, 2016). In BORIS, once the coding process is completed, the program can extract a time-budget for single or grouped observation automatically and present as an at-a-glance summary of the main behaviour features (Friard & Gamba, 2016). Data of behaviour duration and frequency was recorded and conversed to excel files.

2.4 Energy budget

Energy gain We estimated the energy gain of every successful fishing event. First, the prey size was determined by comparing the catch with the beak volume of *M. squamatus* , and was assigned to one of the five following classes: 0.5 volume, 1 volume, 1.5 volume, 2 volume, 2.5 volume of beak (Fig 3). Based on the fish survey at Shangqing River, the average weight of the fish with one beak size was 14.1 g. As the energy content of the fish is approximately 4.0 KJ/g (Gremillet, Schmid, & Culik, 1995) and the assimilation efficiency is assumed to be 80% (Feltham, 1995), the energy gain can then be calculated as:

Energy gained=45.12 x fish size (1)

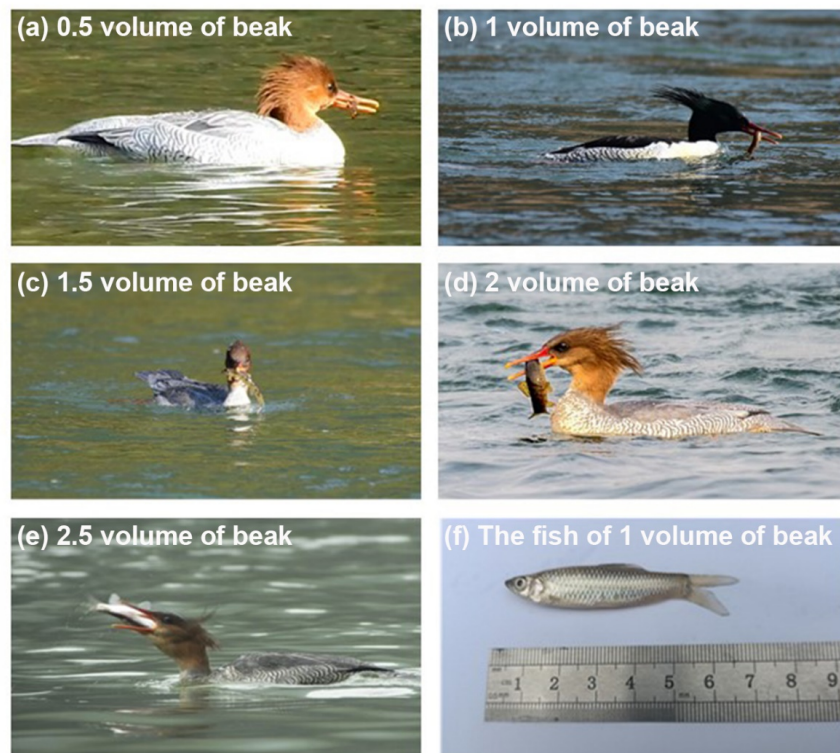


Figure 3. Photos shows fish sizes in relation with the beak of *M. squamatus*. Fish size is used to estimate energy gain.

Energy expenditure Energy expenditure was calculated using the observed foraging activity profile and the Basal Metabolic Rate (BMR). The BMR was determined to use the Aschoff-Pohl equation (Aschoff & Pohl, 1970):

$$\text{BMR} = 307.5 \text{ Body Mass}^{0.734} \quad (2)$$

The BMR coefficients of different behaviours were sourced from the published studies on Common Merganser *Mergus Merganser*, Lesser snow Goose and Black duck (Table 2). Because the BMR coefficient of other activities including socializing, preening and food handling varies greatly from literature, moreover, these activities account for only a small fraction of the total foraging time (less than 4.2% of the total, see Table 3 below), we excluded them in calculating energy balance. The weight data (i.e. male 1125–1400 g, female 870–1100 g) of *M. squamatus* were obtained from (Kear & Hulme, 2005). Therefore, the BMR of male and female *M. squamatus* was calculated as 365.00 KJ/day and 304.12 KJ/day, respectively. We assumed that the mean BMR of *M. squamatus* was 334.56 KJ/day and the energy expenditure was each foraging behaviour BMR by multiplying the behaviour time rate.

Table 2. Published basal metabolic rate (BMR) coefficients of different foraging activities

Behaviour	BMR Coefficient	Species	Reference
Diving	3.2	Common Merganser	(Newson & Hughes, 1998)
Head-dipping	2.5	Lesser Snow Goose	(Jónsson & Afton, 2006)
Eye-submerged	2.0	Lesser Snow Goose	(Jónsson & Afton, 2006)
Vigilance	2.0	Common Merganser	(Newson & Hughes, 1998)
Swimming	2.3	Black Duck	(Beerens, Gawlik, Herring, & Cook, 2011)

2.5 Statistical analyses

To simplify the comparison of behaviour differences in shallow and deep habitat, the eight identified behaviours were group into three main classes (i.e. Fishing, searching, and resting, Table 1). As the three behaviour variables were expressed as a percentage of the total length of foraging bout, they are not independent (i.e. summed to 1), we used generalised multivariate models within Bayesian framework using the R (Team, 2019) package “brms” (Bürkner, 2017). We also we tested three error distribution families: Beta, Gamma, and Gaussian to account for the potentially non-normal distribution. Difference in energy balance was also tested using Bayesian models.

3. Results

During 90 days of the three winters, we obtained a total of 200 effective video footages, which contained 1,086 minutes of 17,995 foraging activities (Table 3). Among these valid for-aging bouts, 84 were in shallow waters habitats and 116 were in deep waters. Of these foraging bouts, we observed 98 successful fishing events. A total of 163 fish were caught as there were occasions that a bird captured more than one in a single foraging bout.

3.1. General pattern of behaviour profiles

Not surprisingly, the birds spent most time in activities relating to obtaining food including diving, head-dipping, eye-submerging, and vigilance, and food handling, preening and other social activities such as intraspecific interaction took only a fraction of a foraging bout (Table 3).

For each foraging activity, diving took the longest time with mean duration of 13.13 seconds (SD = 7.12) followed by swimming (5.22 ± 6.59 s), preening (4.69 ± 4.17 s) and vigilance (4.06 ± 2.69 s), socializing (3.83 ± 3.12 s) and food handling (3.19 ± 4.77 s). While the frequency for head-dipping and eye-submerging were the highest (4.40 ± 5.51 and 5.75 ± 5.48 times/minute, respectively), they took the least time (2.60 ± 0.92 s and 1.89 ± 0.07 s, respectively). Moreover, the standard deviation (SD) of the attributes (i.e. frequency, duration and proportion) for most behaviours were relatively large comparing with the mean, suggesting the highly variable behavioural profiles of the bird.

Table 3. Summary of the foraging behaviours of *M. squamatus* during wintering in Shangqing River, China

Behaviour	No of observations	Frequency (times/min)	Frequency (times/min)	Duration (second)	Duration (second)	Proportion (%)	Proportion (%)
		Mean	SD	Mean	SD	Mean	SD
Eye-submerging	6,857	5.75	5.48	1.89	0.07	18.11	17.25
Head-dipping	5,421	4.40	5.51	2.60	0.92	19.04	23.51
Vigilance	3,032	2.89	1.66	4.06	2.69	19.93	12.60
Diving	1,487	1.48	1.50	13.13	7.12	32.64	28.81
Swimming	693	0.68	0.78	5.22	6.59	5.97	8.64
Handling	162	0.27	0.52	3.19	4.77	2.06	4.69
Preening	240	0.16	0.26	4.69	4.17	1.19	3.02
Social interacting	103	0.09	0.16	3.83	3.12	1.05	1.97

3.2. Foraging behaviors at different habitats

The bird showed distinct behaviour profiles in deep and shallow habitats. While the duration of a foraging bout was only slightly higher in shallow than in deep habitats (Fig. 4A), the proportion of time spent in each activity classes differed significantly. Specifically, while the bird spent significantly more time in getting

ready for fishing in deep waters (Fig. 4B), the time for fishing was significantly greater in shallow waters (Fig. 4C). In addition, time for social interaction was significantly higher in shallow waters (Fig. 4D).

In both habitats, more time was spent for fishing than other activities. In deep waters, the bird spent an average of 62.8%, 36.3% and 0.9% of the foraging time on fishing, preparing, and social interaction, respectively. In shallow waters, the values were 81.8%, 16.8%, and 1.4%. Fishing behaviours were mainly diving (87.3%) in deep water and head-dipping (53.7%) and eye submerging in shallow water (43.1%). Preparing behaviours were mainly vigilance in both deep waters (88.6%) and shallow waters (75.5%).

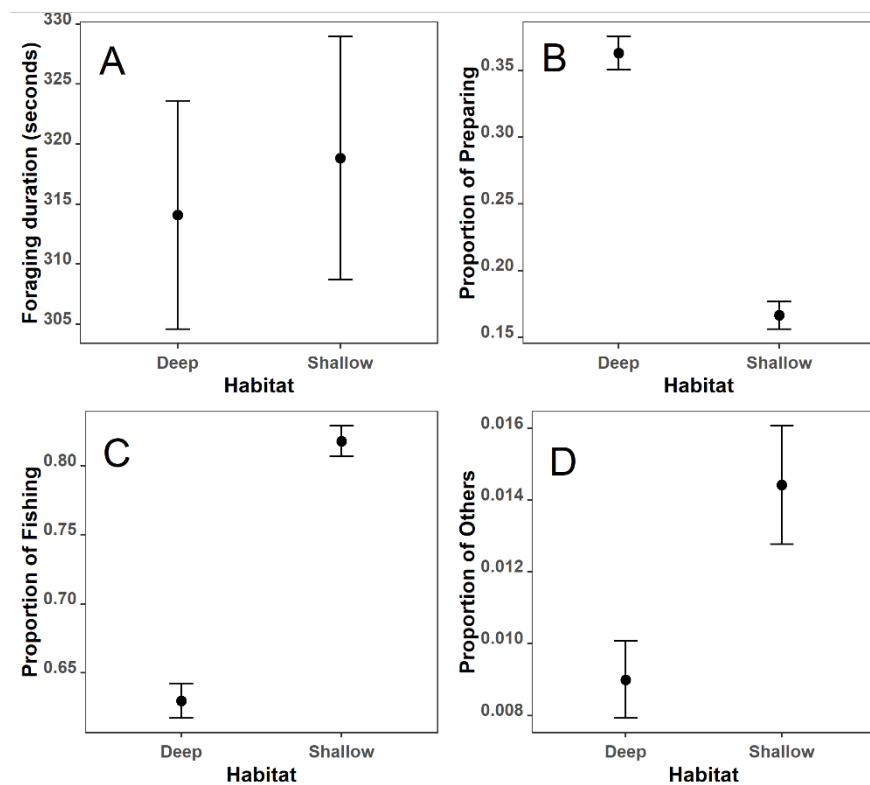


Figure 4. The difference in foraging behaviours of Scaly-sided Merganser *Mergus squamatus* in deep and shallow habitats. The mean (dots) and the 95% credible intervals (vertical bars) are based on 4,000 posterior draws of the fitted models. Note the different scale of Y-axis. A) Foraging duration in seconds; B) Proportion of preparing; C) Proportion of fishing; and D) Proportion of other activities.

3.3. Foraging gain at different water depth

As for the fish caught at different water depth, the mean fish catch rate was 0.28 fish per minute in shallow waters, which is significantly higher than the value of 0.13 fish per minute in deep waters (Fig. 5A). However, as the prey in shallow waters was smaller (data not shown), the mean biomass of the fish captured was slightly greater in deep waters (Fig. 5B).

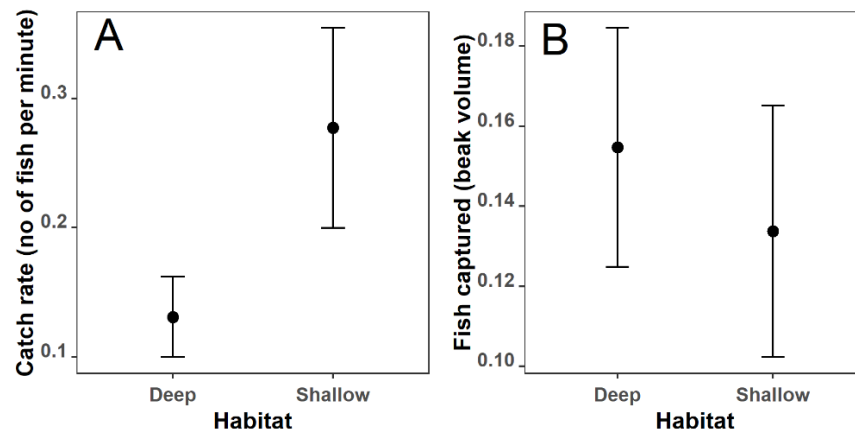


Figure 5. Fish catching rate (A) and biomass of captured fish (B) of the Scaly-sided Merganser *Mergus squamatus* in deep and shallow habitats. The mean (dots) and the 95% credible intervals (vertical bars) are based on 4,000 posterior draws of the fitted models.

3.4. Foraging energetics in shallow and deep waters

Despite the distinct behavioural profiles in different habitats (Fig. 4), the *M. squamatus* showed similar foraging energetics (Fig. 6), suggesting that the birds can fish equally efficiently in both deep and shallow waters. The estimate of mean net energy gains were 6.53 KJ/min and 6.28 KJ/min in deep and shallow habitats, respectively, and the standardized errors (SE) was comparably small (less than 0.50 in both habitats, Fig. 6A). Energy gains through food intake were slightly higher in deep waters (mean estimates were 6.99 KJ/min and 6.08 KJ/min in deep and shallow waters, respectively, Fig. 6B). Again, SE was small in comparison with the mean. The small SE suggested that the bird performed stably during the three winters in both habitats. Although the foraging energy costs were significantly higher in deep waters, this difference did not affect the comparison of energy balance as they were only a fraction of energy gain through food intake (generally less than 5%, Fig. 6C).

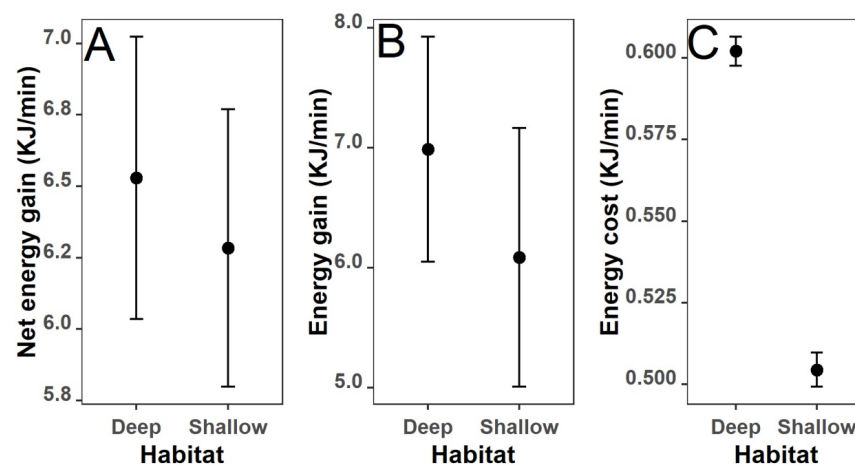


Figure 6. Foraging energetics of Scaly-sided Merganser *Mergus squamatus* in deep and shallow habitats. A) Net energy gain; B) Energy gain from captured prey; and C) Predation cost. The mean (dots) and the 95% credible intervals (vertical bars) are based on 10,000 posterior draws of the fitted models. Note the different scale of Y-axis.

4. Discussion

Animal behavioural traits often show wide and consistent variation among individuals (Dingemanse & Wolf, 2013; Wolf & Weissing, 2012) and this variation has often been suggested to facilitate population persistence in novel and variable environments (Sih et al., 2011). In the context of rapid human-induced environmental change, such as habitat loss and fragmentation, it's urgent to integrate animal behaviour and wildlife conservation studies for maximizing outcomes (Berger-Tal et al., 2019; Greggor et al., 2016; Sutherland, 1998).

We found that the predatory waterbird had similar energetics despite distinct foraging methods, behaviour profiles, and foraging efficiency in shallow- and deep-water habitats. These results suggest that Scaly-sided Merganser is a good example of behavioural flexibility that aligns with expectations of optimum foraging theory (OFT) (Pyke, 1984), in that the duck behaves in accordance to resource availability in different environments, resulting in high foraging efficiency. The behavioural flexibility could be related to evolutionary adaptation (Snell-Rood, 2013).

4.1 Behaviour profiles are distinct

Waterfowls often use special feeding methods when forage in different habitats (Guillemain, Fritz, & Blais, 2000), especially at areas with different water depths. For example, Bewick's swan (*Cygnus columbianus bewickii*) uses head-dipping in shallow waters and upending in deeper areas (Nolet, Fuld, & Van Rijswijk, 2006). We observed that *M. squamatus* used mainly head-dipping in shallow waters and frequent diving in deep waters. On average, *M. squamatus* spent 44% of their foraging time in head-dipping at shallow waters and the proportion of pursuit diving was 55% in deep waters. Similarly, Common Merganser (*Mergus merganser*) immerses their heads to search for prey under the shallow waters with little current and dives repeatedly in deep waters (Anderson, Reeder, & Timken, 1974).

In both environments, majority of the foraging time was allocated to fishing (62.8% and 81.8% in deep waters and shallow waters, Fig. 4). Nevertheless, the bird spent significantly more time in fishing in shallow waters than in deep waters, which may contribute to the observed higher catch rates (Norberg, 1977). Diving was the main activity of fishing behaviours in deep water (87.3%) and mean diving time was 13.13 ± 7.12 s, which was less than the previous studies in Yihuang section, Fuhe River (23.6 ± 6.3 s) and in Wuyuan section, Rao River (18.8 ± 6.0 s) (Shao & Chen, 2017; Shao et al., 2012). The difference of mean diving time might be due to the depth of the river (Carbone & Houston, 1994; Wanless, Harris, & Russell, 1993). Distinct with foraging in deep water, the duration of head-dipping and eye-submerging activities of fishing behaviours in shallow water were high (53.7% and 43.1%). In contrast, more time was spent on preparing in deep waters than in shallow waters. For preparing, vigilance was the main activity in both deep waters (88.6%) and shallow waters (75.5%), and the bird spent significantly more time on vigilance in deep waters than in shallow waters. Most wild animals would allocate more time to maintain high vigilance and reduce other behaviours when encountering disturbances (Fortin, Boyce, Merrill, & Fryxell, 2004; Robinson & Merrill, 2013). As the bird could be more uncertain about the situation surrounding on water surface after diving, more time is required on vigilance in deep waters areas. Previous studied also found that watching-out duration was positively correlated to the previous diving and next diving (Shao, Shi, Zeng, & Jiang, 2014; Ydenberg & Forbes, 1988).

4.2 Food gain and Energy balance is similar

The two feeding strategies (i.e. head-dipping in shallow waters and pursuit diving in deep waters) resulted in significantly different catch rates, and apparently the duck was more efficacious in shallow waters with a catch rates of 0.28 fish/minute (in comparison, the average catch rate was 0.13 fish/minute in deep waters. Fig. 5A). This is in consistency with studies on other piscivorous waterbirds. For example, Shags (*Phalacrocorax aristotelis*) has higher prey-capture performance in shallower (Wanless et al., 1993). The difference in foraging catch rates could be linked to prey abundance and vulnerability, which is strongly affected by water depth (Lantz, Gawlik, & Cook, 2011; Monaghan, Walton, Wanless, Uttley, & Bljrns, 1994; Schekkerman & Beintema, 2007). As the key components of habitat complexity for stream fish, water depth has an important

effect on the distributions and size of fish (Lonzarich & Quinn, 1995; Rose, 2000) and macroinvertebrates as well (Lantz et al., 2011). Small and juvenile fish intended to inhabit shallow waters to avoid predatory fish (Blaber, 1980; Sheaves, 2006). In addition, it would be easier to catch a prey in shallow waters.

Although more fish were caught in shallow waters, the total gains in terms of biomass at different habitats were similar due to the larger size of fish in deep waters. That's to say, the higher prey quality offset the lower prey quantity in deep waters (Brodmann, Reyer, Bollmann, Schlöpfer, & Rauter, 1997), resulting in slightly higher energy gains (6.99 ± 0.94 , and 6.08 ± 1.08 KJ/minute in deep waters and shallow waters, respectively, Fig. 6B). However, the energy gains in shallow waters may be underestimated as macroinvertebrates were excluded in the study due to technical difficulty, and predation of macroinvertebrates mainly occurs in shallow habitats.

Different foraging patterns imply highly different energy costs (Godfrey & Bryant, 2000). In deep waters, the bird spent significantly more time in diving, which has high basal metabolic rate (Table 1 and (Leeuw, 1996)). The frequent pursuit diving resulted in significantly higher energy cost in deeper water (Fig. 6C). However, as the foraging energy consumption of *M. squamatus* was only a fraction of energy intake (less than 10%), it had little influence on the foraging energetics: the net energy gain was slightly higher in deep waters but the difference was not statistically significant (Fig. 6C).

4.3 Optimal foraging theory

Predatory animals may have a series of alternative foraging modes (Kuwae, Miyoshi, Sassa, & Watabe, 2010). The optimal foraging theory (Pyke, 1984) predicts that decisions on foraging strategy, including what, where and how to hunt, are based on a maximization of currencies (Bautista, Tinbergen, & Kacelnik, 2001). Therefore, in their natural habitat, predators are expected to take different foraging strategies in response to both prey abundance and vulnerability such that they attain the highest energy intake rate.

As predicted by OPT, *M. squamatus* showed high behavioural flexibility by adjusting its foraging methods and behavior profiles in shallow and deep areas. In deep waters, where prey abundance and vulnerability are lower, *M. squamatus* allocated most of the time to repeated pursuit diving to minimize the foraging energy cost. This strategy was awarded with bigger gains and resulting in comparable energy gain as in shallow waters, where smaller preys are more abundant and easier to catch. The wintering grounds of *M. squamatus* are mainly mountainous streams (Zhao & Pao, 1998), which resources are patchily distributed (Taylor & Warren Jr, 2001). The behavioural flexibility is critical for predators foraging in heterogeneous environment (Abrahms et al., 2020), where prey is patchily distributed and may be unpredictable for diving birds (Tessier & Bost, 2020).

5. Management implications and conclusions

Overall, our findings highlight that the wintering *M. squamatus* has high behavioural flexibility adapted to the heterogeneous foraging environment. However, its population is decreasing continuously in recent decades and is listed as globally endangered by the IUCN (BirdLife & International, 2017). This gives an indication that the rapid anthropogenic environmental changes may be exceeding or even have exceeded the adaptive capacity of the species (Sih et al., 2011). *M. merganser* prefers to forage in clear, flowing river reaches with relatively shallow waters depth (less than 10 m), which provide diverse microhabitats, such as pools, glides, riffles, sand/gravel bars, and islands, for fish and benthic macroinvertebrates (Aadland, 1993). *M. merganser* is morphologically specialized in hunting moving prey in such environment (Kondratyev, 1999). The evolutionary adaptation could lose its competitive advantages as human pressures on existing habitats intensified (Lei et al., 2019) with increasing water resource developments and other activities such as sanding mining and fishing. These human pressures could dramatically change the river landscape and decrease prey abundance. For example, river regulation by damming increases water depth and reduces habitat heterogeneity (Lei et al., 2019; Swales, 2018; Zeng, Lu, et al., 2018). The endangered status of this iconic species demands researches on estimating how much habitat, of what quality, is required to sustain its population.

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References

- Aadland, L. P. (1993). Stream habitat types: their fish assemblages and relationship to flow. *North American Journal of Fisheries Management*, 13 (4), 790-806.
- Abrahms, B., Aikens, E. O., Armstrong, J. B., Deacy, W. W., Kauffman, M. J., & Merkle, J. A. (2020). Emerging perspectives on resource tracking and animal movement ecology. *Trends in ecology evolutionary applications*, 36 (4), 308-320.
- Aletta, F., Lepore, F., Kostara-Konstantinou, E., Kang, J., & Astolfi, A. (2016). An experimental study on the influence of soundscapes on people's behaviour in an open public space. *Applied sciences*, 6 (10), 276.
- Anderson, B. W., Reeder, M. G., & Timken, R. L. (1974). Notes on the feeding behavior of the Common Merganser (*Mergus merganser*). *The Condor*, 76 (4), 472-476.
- Aschoff, J., & Pohl, H. (1970). Der ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergröße. *Journal of Ornithology*, 111 (1), 38-47.
- Barbarossa, V., Schmitt, R. J., Huijbregts, M. A., Zarfl, C., King, H., & Schipper, A. M. (2020). Impacts of current and future large dams on the geographic range connectivity of freshwater fish worldwide. *Proceedings of the National Academy of Sciences*, 117 (7), 3648-3655.
- Bautista, L. M., Tinbergen, J., & Kacelnik, A. (2001). To walk or to fly? How birds choose among foraging modes. *Proceedings of the National Academy of Sciences*, 98 (3), 1089-1094.
- Beerens, J. M., Gawlik, D. E., Herring, G., & Cook, M. I. (2011). Dynamic habitat selection by two wading bird species with divergent foraging strategies in a seasonally fluctuating wetland. *The Auk*, 128 (4), 651-662.
- Berger-Tal, O., Greggor, A. L., Macura, B., Adams, C. A., Blumenthal, A., Bouskila, A., Gotanda, K. M. (2019). Systematic reviews and maps as tools for applying behavioral ecology to management and policy. *Behavioral Ecology*, 30 (1), 1-8.
- BirdLife International. (2017). *Mergus squamatus* (amended version of 2017 assessment). The IUCN Red List of Threatened Species 2017: e.T22680488A118860238.
- Blaber, S. (1980). Fish of Trinity Inlet system of north Queensland with notes on the ecology of fish faunas of tropical Indo-Pacific estuaries. *Marine Freshwater Research*, 31 (2), 137-146.
- Brodmann, P. A., Reyer, H.-U., Bollmann, K., Schläpfer, A. R., & Rauter, C. (1997). The importance of food quantity and quality for reproductive performance in alpine water pipits (*Anthus spinoletta*). *Oecologia*, 109 (2), 200-208.
- Bruijn, J. A. C. d., Vosteen, I., Vet, L. E. M., Smid, H. M., & Boer, J. G. d. (2021). Multi-camera field monitoring reveals costs of learning for parasitoid foraging behaviour. *Journal of Animal Ecology*, 90 , 1635-1646.

- Burkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of statistical software*, 80 (1), 1-28.
- Carbone, C., & Houston, A. (1994). Patterns in the diving behaviour of the pochard, *Aythya ferina* : a test of an optimality model. *Animal Behaviour*, 48 (2), 457-465.
- Dingemanse, N. J., & Wolf, M. (2013). Between-individual differences in behavioural plasticity within populations: causes and consequences. *Animal Behaviour*, 85 (5), 1031-1039.
- Dudgeon, D. (2019). Multiple threats imperil freshwater biodiversity in the Anthropocene. *Current Biology*, 29 (19), R960-R967.
- Feltham, M. (1995). Consumption of Atlantic salmon smolts and parr by goosanders: estimates from doubly-labelled water measurements of captive birds released on two Scottish rivers. *Journal of Fish Biology*, 46 (2), 273-281.
- Fortin, D., Boyce, M. S., Merrill, E. H., & Fryxell, J. M. (2004). Foraging costs of vigilance in large mammalian herbivores. *Oikos*, 107 (1), 172-180.
- Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in ecology evolution*, 7 (11), 1325-1330.
- Gilmour, M. E., Castillo-Guerrero, J. A., Fleishman, A. B., Hernandez-Vazquez, S., Young, H. S., & Shaffer, S. A. (2018). Plasticity of foraging behaviors in response to diverse environmental conditions. *Ecosphere*, 9 (7), e02301.
- Giraldo, C., Ernande, B., Cresson, P., Kopp, D., Cachera, M., Travers-Trolet, M., & Lefebvre, S. (2017). Depth gradient in the resource use of a fish community from a semienclosed sea. *Limnology Oceanography*, 62 (5), 2213-2226.
- Godfrey, J., & Bryant, D. (2000). State-dependent behaviour and energy expenditure: an experimental study of European robins on winter territories. *Journal of Animal Ecology*, 69 (2), 301-313.
- Greggor, A. L., Berger-Tal, O., Blumstein, D. T., Angeloni, L., Bessa-Gomes, C., Blackwell, B. F., Fernandez-Juricic, E. (2016). Research priorities from animal behaviour for maximising conservation progress. *Trends in ecology evolutionary applications*, 31 (12), 953-964.
- Gremillet, D., Schmid, D., & Culik, B. (1995). Energy requirements of breeding great cormorants *Phalacrocorax carbo sinensis*. *Marine ecology progress series*, 121 , 1-9.
- Guillemain, M., Fritz, H., & Blais, S. (2000). Foraging methods can affect patch choice: an experimental study in Mallard (*Anas platyrhynchos*). *Behavioural processes*, 50 (2-3), 123-129.
- Hadfield, M., & Strathmann, M. (1996). Variability, flexibility and plasticity in life histories of marine invertebrates. *Oceanologica acta*, 19 (3-4), 323-334.
- Harvey, B., & Stewart, A. (1991). Fish size and habitat depth relationships in headwater streams. *Oecologia*, 87 (3), 336-342.
- He, F., Zarfl, C., Bremerich, V., David, J. N., Hogan, Z., Kalinkat, G., Jahnig, S. C. (2019). The global decline of freshwater megafauna. *Global Change Biology*, 25 (11), 3883-3892.
- Jonsson, J. E., & Afton, A. D. (2006). Different time and energy budgets of Lesser Snow Geese in rice-prairies and coastal marshes in southwest Louisiana. *Waterbirds*, 29 (4), 451-458.
- Kear, J., & Hulme, M. (2005). Ducks, geese and swans: Species accounts (*Cairina* to *Mergus*) (Vol. 2): Oxford University Press.
- Kondratyev, A. V. (1999). Foraging strategies and habitat use of sea ducks breeding in northeast Russia. *Ccasional Papers-Canadian Wildlife Service* , 51-58.

- Kuwae, T., Miyoshi, E., Sassa, S., & Watabe, Y. (2010). Foraging mode shift in varying environmental conditions by dunlin *Calidris alpina*. *Marine ecology progress series*, 406 , 281-289.
- Lantz, S. M., Gawlik, D. E., & Cook, M. I. (2011). The effects of water depth and emergent vegetation on foraging success and habitat selection of wading birds in the Everglades. *Waterbirds: The International Journal of Waterbird Biology*, 34 (4), 439-447.
- Leeuw, J. J. d. (1996). Diving costs as a component of daily energy budgets of aquatic birds and mammals: generalizing the inclusion of dive-recovery costs demonstrated in tufted ducks. *Canadian Journal of Zoology*, 74 (12), 2131-2142.
- Lei, J., Jia, Y., Wang, Y., Lei, G., Lu, C., Saintilan, N., & Wen, L. (2019). Behavioural plasticity and trophic niche shift: How wintering geese respond to habitat alteration. *Freshwater Biology*, 64 (6), 1183-1195.
- Lonzarich, D. G., & Quinn, T. P. (1995). Experimental evidence for the effect of depth and structure on the distribution, growth, and survival of stream fishes. *Canadian Journal of Zoology*, 73 (12), 2223-2230.
- Monaghan, P., Walton, P., Wanless, S., Uttley, J., & Bljns, M. (1994). Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding guillemots *Uria aalge*. *Ibis*, 136 (2), 214-222.
- Newson, S. E., & Hughes, B. (1998). Diurnal activity and energy budgets of Goosander *Mergus merganser* wintering on Chew Valley Lake, North Somerset: influence of time of day and sex. *Wildfowl*, 49 (49), 173-180.
- Nolet, B. A., Fuld, V. N., & Van Rijswijk, M. E. (2006). Foraging costs and accessibility as determinants of giving-up densities in a swan-pondweed system. *Oikos*, 112 (2), 353-362.
- Norberg, R. A. (1977). An ecological theory on foraging time and energetics and choice of optimal food-searching method. *The Journal of Animal Ecology*, 46 (2), 511-529.
- Pyke, G. H. (1984). Optimal foraging theory: a critical review. *Annual review of Ecology Systematics*, 15 (1), 523-575.
- Robinson, B. G., & Merrill, E. H. (2013). Foraging–vigilance trade-offs in a partially migratory population: comparing migrants and residents on a sympatric range. *Animal Behaviour*, 85 (4), 849-856.
- Rose, K. A. (2000). Why are quantitative relationships between environmental quality and fish populations so elusive? *Ecological Applications*, 10 (2), 367-385.
- Schekkerman, H., & Beintema, A. J. (2007). Abundance of invertebrates and foraging success of Black-tailed Godwit *Limosa limosa* chicks in relation to agricultural grassland management. *Ardea*, 95 (1), 39-54.
- Schmidt-Nielsen, K. (1997). *Animal physiology: adaptation and environment* : Cambridge university press.
- Schoener, T. W. (1971). Theory of feeding strategies. *Annual review of Ecology Systematics*, 2 (1), 369-404.
- Shao, M., & Chen, B. (2017). Effect of sex, temperature, time and flock size on the diving behavior of the wintering Scaly-sided Merganser (*Mergus squamatus*). *Avian Research*, 8 (1), 1-7.
- Shao, M., Shi, W., Zeng, B., & Jiang, J. (2014). Diving Behavior of Scaly-sided Merganser, *Mergus squamatus* in Poyang Lake watershed, China. *Pakistan Journal of Zoology*, 46 (1), 284-287.
- Shao, M., Zeng, B., Tim, H., Chen, L., You, C., Wang, H., & Dai, N. (2012). Winter ecology and conservation threats of scaly-sided Merganser *Mergus squamatus* in Poyang Lake watershed, China. *Pakistan Journal of Zoology*, 44 (2), 503-510.
- Sheaves, M. (2006). Scale-dependent variation in composition of fish fauna among sandy tropical estuarine embayments. *Marine ecology progress series*, 310 , 173-184.

- Sih, A., Ferrari, M. C., & Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary applications*, 4 (2), 367-387.
- Snell-Rood, E. C. (2013). An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behaviour*, 85 (5), 1004-1011.
- Solovieva, D. (2013). Foraging behaviour and daily time budget of Scaly-sided Merganser *Mergus squamatus* breeding on Iman River, Russia. *Wildfowl*, 53 (53), 205-214.
- Sutherland, W. J. (1998). The importance of behavioural studies in conservation biology. *Animal Behaviour*, 56 (4), 801-809.
- Swales, S. (2018). The Use of Instream Habitat Improvement Methodology Inmitigating the Adverse Effects of River Regulation on Fisheries. In *Alternatives in regulated river management* (pp. 185-208): CRC Press.
- Taylor, C. M., & Warren Jr, M. L. (2001). Dynamics in species composition of stream fish assemblages: environmental variability and nested subsets. *Ecology*, 82 (8), 2320-2330.
- R development core Team. (2019). A Language and Environment for Statistical Computing, version 3.6.1.; R Foundation for Statistical Computing: Vienna, Austria.
- Tessier, E., & Bost, C.-A. (2020). Behavioural adjustments during foraging in two diving seabirds: king and macaroni penguins. *Marine Biology*, 167 (9), 1-11.
- Tonkin, J. D., Heino, J., & Altermatt, F. (2018). Metacommunities in river networks: The importance of network structure and connectivity on patterns and processes. *Freshwater Biology*, 63 (1), 1-5.
- Tunney, T. D., & Steingrimsson, S. O. (2012). Foraging mode variation in three stream-dwelling salmonid fishes. *Ecology of Freshwater Fish*, 21 (4), 570-580.
- Van Buskirk, J., Candolin, U., & Wong, B. (2012). *Behavioural plasticity and environmental change* : Oxford University Press.
- Wang, Z., Shan, J., Li, Y., Tu, X., Jia, D., Hao, X., Zhao, J. (2010). Winter population status and endangered factors of scaly-sided merganser (*Mergus squamatus*) in Jiangxi Province. *Sichuan J. Zool*, 29 , 597-600.
- Wanless, S., Harris, M., & Russell, A. (1993). Factors influencing food-load sizes brought in by Shags *Phalacrocorax aristotelis* during chick rearing. *Ibis*, 135 (1), 19-24.
- West-Eberhard, M. J. (1989). Phenotypic plasticity and the origins of diversity. *Annual review of Ecology Systematics*, 20 (1), 249-278.
- Wolf, M., & Weissing, F. (2012). Animal personalities: consequences for ecology and evolution. *Trends in ecology*, 27 (8), 452-461.
- Wong, B., & Candolin, U. (2015). Behavioral responses to changing environments. *Behavioral Ecology*, 26 (3), 665-673.
- Ydenberg, R., & Forbes, L. (1988). Diving and foraging in the Western Grebe. *Ornis Scandinavica*, 19 (2), 129-133.
- Zeng, Q., Lu, C., Li, G., Guo, Z.-B., Wen, L., & Lei, G.-C. (2018). Impact of a dam on wintering waterbirds' habitat use. *Environmental Conservation*, 45 (4), 307-314.
- Zeng, Q., Shi, L., Wen, L., Chen, J., Duo, H., & Lei, G. (2015). Gravel bars can be critical for biodiversity conservation: A case study on Scaly-sided Merganser in South China. *PLoS One*, 10 (5), 1-13.
- Zeng, Q., Wei, Q., & Lei, G. (2018). Contribution of citizen science towards cryptic species census: “many eyes” define wintering range of the Scaly-sided Merganser in mainland China. *Avian Research*, 9 (01), 63-72.

Zhang, S., Ma, Z., Choi, C., Peng, H., Melville, D. S., Zhao, T., Gils, J. A. (2019). Morphological and digestive adjustments buffer performance: How staging shorebirds cope with severe food declines. *Ecology evolutionary applications*, 9 (7), 3868-3878.

Zhao, Z., & Pao, Z. (1998). The foraging behaviour of the Scaly-sided Merganser *Mergus squamatus* in the Changbai Mountains and Xiao Xingangling Mountains of China. *Forktail*, 14 , 76-77.