

# Feeding strategies of Red Knots (*Calidris canutus canutus*) in their tropical wintering grounds of Banc d'Arguin, Mauritania

## 1. Introduction

There is a huge amount of variation in the way animals search for food. Traditionally, optimal foraging models assumed that the maximization of net energy or protein intake was the primary goal of foragers (Stephens & Krebs 1987). Within this framework two different foraging behaviours can be distinguished. There is a generalist strategy, which ingests all prey items encountered and there is a specialist strategy, where only single type of prey is ingested. If prey items are encountered one at the time, a specialist, which rejects poor prey items to continue searching for more profitable ones, might achieve a higher intake rate than a generalist. Prey choice is often evaluated at a species or population level, while the variation between individuals is overlooked (Bolnick *et al.* 2003). In octopuses, a generalist species, several individuals were found to specialize in in certain prey items (Mather *et al.* 2012). It is thus possible for a generalist species to consist of both generalist individuals and specialist individuals.

The red knot (*Calidris canutus*), a midsized shorebird, is believed to be a specialist, foraging on molluscs (Davidson & Piersma 1992; Piersma 1994). Prey items (ranging from 9 to 16 mm) are ingested whole and crushed in their muscular gizzard to access the flesh within the shells (Dekinga *et al.* 2001; van Gils *et al.* 2003). In the Dutch Wadden Sea , they feed predominantly on *Limecola balthica* and snail species (Boere & Smit 1981; Zwarts & Blomert 1992), and to a lower extent also: *Mya arenaria*, *Mytilus edulis* and *Cerastoderma edule* (Zwarts & Blomert 1992).

The canutus subspecies only uses the Wadden Sea as a stopover site during migration. It's wintering grounds are further south, mainly the Banc d'Arguin in Mauritania. Around two million shorebirds use the Banc d'Arguin as wintering site (Smith & Piersma 1989; Oudman *et al.* 2020). Of these, the knot is declining in numbers with currently around 200.000 individuals left (Ahmedou Salem *et al.* 2014; Oudman *et al.* 2020). The intertidal area is covered extensively by *Zostera noltii* (hereafter *Zostera*) seagrass beds at about 85% (Wolff & Smit 1990). This makes the area of great ecological value as seagrass beds provide food and shelter for benthic species, trap and recycle nutrients and stabilise the seabed (Larkum *et al.* 2006). More invertebrate species occur in the seagrass beds than

in bare mudflats (Wijnsma *et al.* 1999). This leads to more shorebirds being present in the seagrass beds compared to the bare mudflats (Altenburg *et al.* 1982). An extensive survey by Ahmedou Salem *et al.* (2014) showed that the most abundant bivalves in the area are *Loripes orbiculatus* (hereafter *Loripes*), *Dosinia isocardia* (hereafter *Dosinia*) and *Senilia senilis*. This corresponds with knot diet as *Loripes* and *Dosinia* are eaten the most (van Gils *et al.* 2012, 2013). However, they also eat *Zostera* seagrass roots and rhizomes which are believed to be poor quality food (Pérez-Lloréns *et al.* 1991).

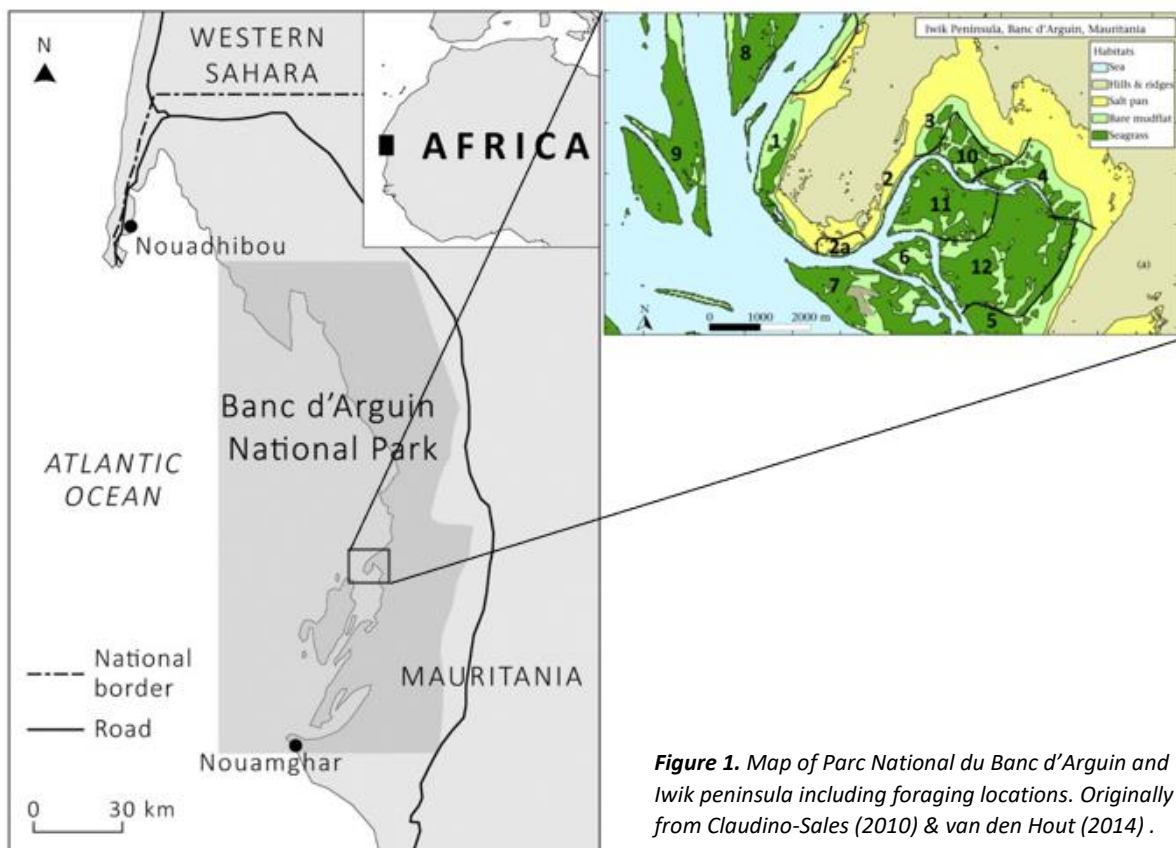
The canutus subspecies breeds in the Arctic tundra of the Taimyr peninsula, Russia. There, their breeding is affected by climate change. Climate change affects species worldwide in multiple ways. It is possible for species to go extinct or to change their geographical distribution (Visser & Both 2005). It is also possible that they adapt to the new environmental conditions (Teplitsky & Millien 2014). In many organisms, one adaptation is the shrinkage of body size, because smaller individuals dissipate body heat better due to their increased surface to volume ratio and are thus better able to cope with increased temperatures (Gardner *et al.* 2011). Another form of body shrinkage stems from decreased nutrition of an animal in its juvenile stage (Metcalf & Monaghan 2001). This might be true for knots as well. van Gils *et al.* (2016) describe a possible shift in food abundance due to earlier snow melt in their breeding grounds as a result of climate change. In years with an early snowmelt, the arthropod food peak might no longer correspond with the hatching date of knot chicks. This way there might be less food available for the chicks, possibly leading to a reduced growth. It was found that years with earlier snowmelt resulted in chicks with smaller body sizes. Alongside a smaller body size their bill might also be shorter. This might affect their diet in the adult life stage as their most abundant prey item in the wintering grounds, *Loripes*, is buried relatively deep in the sediment, mostly out of reach of shorter billed knots. They have to rely on the less abundant *Dosinia* and *Zostera* rhizomes of less quality. It is thus possible that climate change in the Arctic has fitness consequences for knots in their tropical wintering grounds.

It is yet unclear if knots specialize in certain prey types such as bivalves or seagrass rhizomes or that they can be considered generalists in the Banc d'Arguin. Their diet is investigated to reveal differences regarding prey choice. The correlation between bill length and diet as described by van Gils *et al.* (2016) is also investigated. I aim to answer the following research questions (1) are individual knots consistent in their diet choice? (2) Can their diet be explained by bill length? My hypothesis is that (1) knots show a distinct feeding strategy for either seagrass or bivalves so they can specialize in foraging for a single prey type, (2) longer billed knots show a preference for bivalves and can thus be considered specialist, whereas shorter billed knots have to complement their diet

with seagrass rhizomes as they have less access to bivalves due to them being buried deeper in the sediment and can thus be considered generalists.

## 2. Methods

During an expedition in late 2019, foraging adult knots were filmed at the Parc National du Banc d'Arguin, Mauritania (**Fig. 1**). Only previously caught birds with colour rings were filmed from a known colour ringed population. This way their bill length, sex and tarsus length is known and their diet at the moment of capture was determined by stable isotope analysis of blood samples. At the start of filming the location of knots on the mudflat was also determined as the intertidal area consists of different mudflats separated by gullies and subtidal mudflats (**Fig. 1**). Only birds that were filmed for over 10 minutes were analysed using BORIS software (Friard & Gamba 2016). The behaviour can be divided in several classes (**Table 1**). Foraging was divided into searching, handling and ingesting. The searching behaviour consisted of probing, pecking and sweeping. Handling was divided by the food type that was handled which consisted of bivalves, seagrass, mud snails, shrimp and unknown prey items. Ingesting determined whether a prey item was swallowed or rejected. The output data was further analysed using R (version 4.1.0) software (R Core Team 2019). Only videos with at least 5 ingests were analysed as a minimum amount of ingests is needed to determine



**Figure 1.** Map of Parc National du Banc d'Arguin and Iwik peninsula including foraging locations. Originally from Claudino-Sales (2010) & van den Hout (2014) .

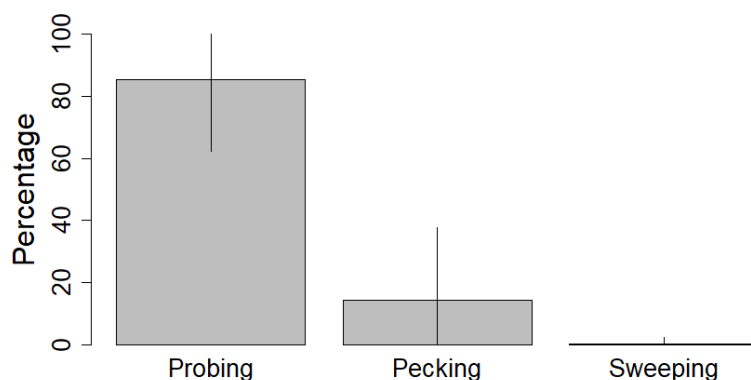
**Table 1.** Ethogram used to analyse videos. Behaviour code shows the type of behaviour. Behaviour type shows if a behaviour code is a continuous behaviour (state event) or a single behaviour (point event).

| Behaviour code     | Behaviour type | Description  |
|--------------------|----------------|--|
| Searching          | State event    | Bird is probing, pecking or sweeping te sediment with its bill   |
| Handeling          | State event    | Bird is handeling a food item: seagrass, bivalve, mud snail, shrimp, unknown   |
| Ingesting          | Point event    | Bird is swallowing or rejecting a prey item: swallow, rejection, unknown   |
| Not searching      | State event    | Bird is not searching for food but showing other types of behavior: walking, vigilance, preening, drinking, scratching, flying, bathing, resting   |
| Out of sight       | State event    | Unable to identify bird behaviour  |
| Social interaction | State event    | Bird shows a social interaction with another bird where the recieving bird has a prey item, winning prey not won, winning prey won, losing prey lost, losing prey not lost.<br>Or the receiving bird has no prey item, winning no prey, losing no prey |
| Step               | Point event    | Bird takes a single step   |
| Defecate           | Point event    | Bird is defecating   |
| Sip                | Point event    | Bird takes one sip while drinking  |

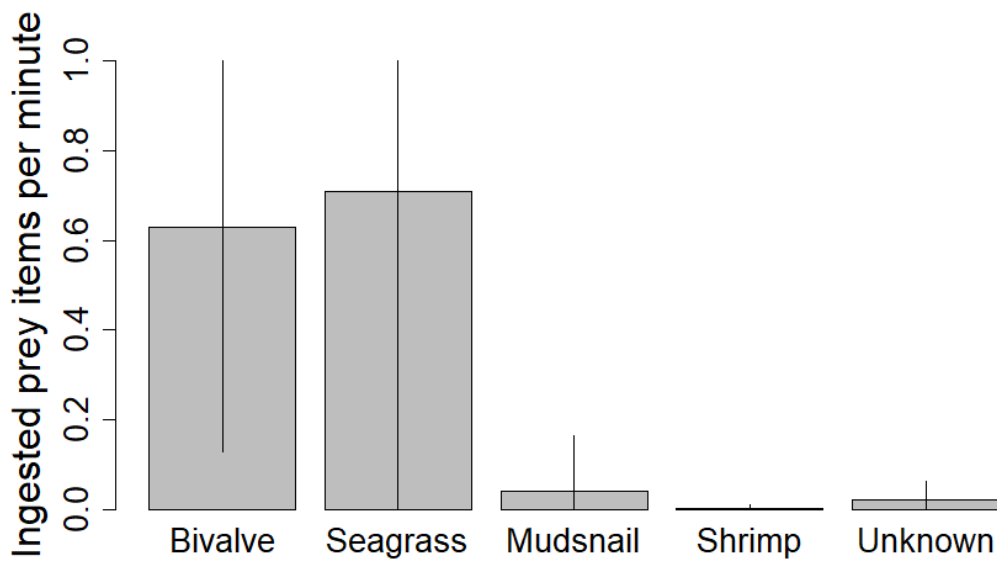
the diet. If at least 80% of the diet consisted of a single food type the individual was considered a specialist. An ANOVA was used to test whether diet composition differed between knots. Variation in the knot diet was analysed using a beta regression model from the betareg package using bill length, sex, wingspan and foraging location as predictor variables (Cribari-Neto & Zeileis 2010). All possible combinations between predictor variables and a null model were compared using AIC model selection (Sakamoto *et al.* 1986). The best fit model was determined as the model with the lowest AIC score. When AIC scores fell within two points the model with the least amount of predictor variables was chosen as the model with the best fit. To compare the different mudflat areas, a Tukey HSD test is used to check which areas differed from each other.

### 3. Results

During the expedition 39 individual knots were filmed for at least 10 minutes. Several birds were filmed multiple times resulting in 63 videos that were analysed. 68% of the total time across all knots was spent foraging. Probing was the most dominant foraging behaviour (**Fig. 2**). Knots also displayed pecking behaviour, but at a lower frequency compared to probing. Only one knot displayed



**Figure 2.** The total amount of time knots spent foraging divided in the three foraging behaviour classes.



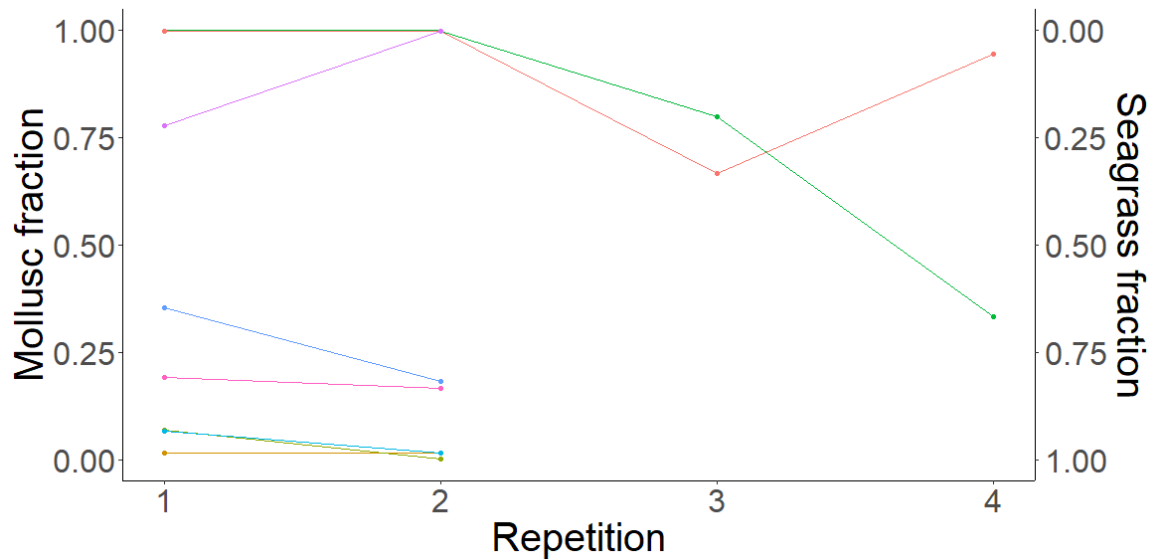
**Figure 3.** Total food intake of all knots combined.



**Figure 4.** Diet composition of individual knots as a percentage of their total diet. Dashed line indicates the average population diet.

sweeping behaviour. Bivalves and seagrass rhizomes were the most eaten prey items (**Fig. 3**). Shrimp were eaten sporadically but never dominated the diet. Mud snails only dominated the diet in one bird. Bivalves were combined with mud snails in a new prey item group called molluscs for further analyses, shrimp and unidentified prey were left out. This way, the diet composition can be analysed as the fraction of molluscs and seagrass rhizomes of the total diet. 18 knots fed predominantly on molluscs (mollusc % > 0.8) while 8 knots fed predominantly on seagrass (mollusc % < 0.2) (**Fig. 4**). This amounts to 2/3 of the observed population being considered specialists and 1/3 generalists. An ANOVA test showed a difference in diet composition between knots ( $p < 0.001$ )(**Fig. 5**). Seagrass eating knots were quite consistent in their feeding behaviour. Bivalve eating knots shifted their diet somewhat, but never to a seagrass only diet. The null model was the model with the least amount of predictor variables and the best fit (**Table 2**). Bill length did not explain the variation in the knot diet

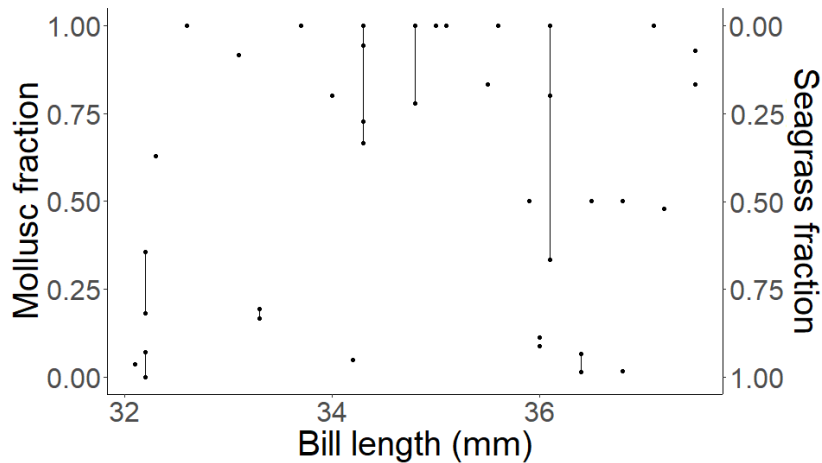
(Fig. 6). A beta regression showed no relationship between the bill length and the diet composition ( $p = 0.973$ ). Despite the null model having the best fit, the mudflat area might still explain some of the data. In the model  $\sim S+A$  the diet composition of knots differed between mudflat areas, where area 1 differed significantly from area 6 and 7 ( $p = 0.017$  and  $p = 0.021$  respectively).



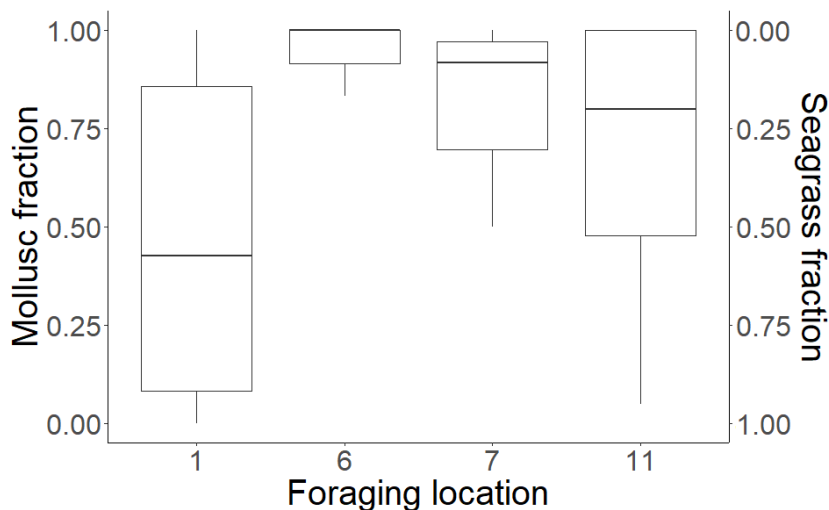
**Figure 5.** Change in diet composition between videos of knots that were filmed multiple times. Variation between individuals was larger than within individuals (ANOVA  $p < 0,001$ ).

| Model          | K | AIC    | $\Delta AIC$ |
|----------------|---|--------|--------------|
| $\sim 1$       | 1 | -66.07 |              |
| $\sim S+A$     | 3 | -64.93 | -1.14        |
| $\sim A$       | 2 | -64.76 | -1.3         |
| $\sim S$       | 2 | -64.54 | -1.53        |
| $\sim B$       | 2 | -64.32 | -1.75        |
| $\sim T$       | 2 | -64.08 | -1.99        |
| $\sim B+S+A$   | 4 | -63.33 | -2.74        |
| $\sim T+A$     | 3 | -63.03 | -3.04        |
| $\sim B+S$     | 3 | -63    | -3.07        |
| $\sim S+T+A$   | 4 | -62.93 | -3.14        |
| $\sim B+A$     | 3 | -62.84 | -3.23        |
| $\sim S+T$     | 3 | -62.68 | -3.39        |
| $\sim B+T$     | 3 | -62.32 | -3.75        |
| $\sim B+S+T+A$ | 5 | -61.39 | -4.68        |
| $\sim B+T+A$   | 4 | -61.23 | -4.84        |
| $\sim B+S+T$   | 4 | -61.04 | -5.03        |

**Table 2.** Output of the beta regression model with predictor variables Bill length (B), Sex (S), Tarsus length (T) and mudflat area (A).



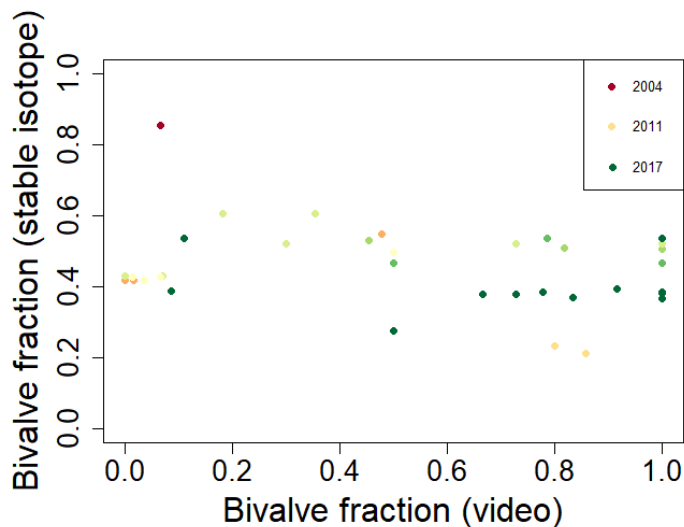
**Figure 6.** Relationship between knot diet and bill length. Connected dots represent individual birds that were filmed multiple times. No correlation was found ( $p = 0.973$ ).



**Figure 7.** Fraction of bivalves in knot diet per mudflat area. Area 1 had 28 values, area 6 had 4 values, area 7 had 10 values, area 11 had 5 values and area 9 had 1 values which was left out of the analyses. Beta regression showed a significant difference between area 1 and 6 ( $p = 0.017$ ) and area 1 and 7 ( $p = 0.021$ ).

#### 4. Discussion

The distribution of prey choice was skewed towards both extremes, meaning a diet dominated by either molluscs and seagrass rhizomes was more abundant (**Fig. 4**). Moreover, the diet of knots that were filmed multiple times remained largely consistent, especially for seagrass eating knots (**Fig. 5**). Most knots thus tend to specialize in a mollusc or seagrass based diet. However, the underlying factors of why some knots specialize in molluscs or seagrass remains unanswered, among which the length of their bill. This is in contradiction with van Gils *et al.* (2016) who found an increase in *Loripes* in the diet of longer billed knots. The diet in van Gils *et al.* (2016) was determined using stable



**Figure 8.** Comparison of the diet determined in this study (x axis) and the article by van Gils *et al.* (2016) (y axis). Colour determines the year in which the stable isotope samples were taken.

isotope analyses at the moment of capture. Because the same knots were analysed in that article and this study, the results can be compared. The diet resulting from the stable isotope analysis is compared to the diet resulting from this study. The proportion of bivalves between the two studies did not correlate (**Fig. 8**). There are however several key differences between van Gils *et al.* (2016) and this study. First, the methodology to determine diet was different. As aforementioned van Gils *et al.* (2016) determined the diet by stable isotope analysis. This way, the diet can be constructed over a long period of time. This study used diet determination by video analysis, which only looks at the diet over a period of around 15 minutes. Second, the measurements were not taken at the same time. While all videos were shot in late 2019 the stable isotope samples were taken in different years. At the earliest in 2004 and at the latest in 2017. This might hint at the fact that knots shift their diet between years. Third, using the stable isotope method it is possible to determine the diet of bivalves at the species level. The article by van Gils *et al.* (2016) showed that mainly the proportion of *Loripes* in the diet increased with bill length. With video analysis it is impossible to differentiate the ingested bivalves at the species level. While the proportion of bivalves overall did not change depending on bill length it is possible that the proportion of *Loripes* and *Dosinia* do.

None of the studied predictor variables were able to explain differences in knot diet (**Table 2**). However, differences in diet between foraging locations were found (**Fig. 7**). At foraging locations 1 and 11 both seagrass and mollusc eating knots were present while at foraging locations 6 and 7 mainly mollusc eating knots were present. These foraging locations are at different distances from the coastline (**Fig. 1**). Van den Hout *et al.* (2014) describes a higher predation pressure closer to the coastline resulting in knots spending more time staying vigilant there. It is interesting to note that at foraging location 1, closest to the coastline, knots eat both seagrass and mollusc whereas only



mollusc eating knots are found at foraging location 6 and 7 further away from the coastline. It is thus possible that predation pressure affects knot diet. Van den Hout *et al.* (2014) also shows that mainly juvenile knots forage near the coast as they are displaced by adults at locations further seaward. An age related component might thus also influence knot diet.

Despite probing being the most used foraging behaviour, pecking could still have contributed to the overall food intake (**Fig. 2**). As pecking is a visual form of foraging, mostly mud snails residing on the top of the sediment are predated. Including pecking in the overall food intake might impact the number of ingested mud snails. The fact that it was left out is a limitation that is recognized. Overall, our results show that knots tend to specialize in either a mollusc or seagrass diet. This pattern remained consistent for knots that were filmed multiple times.

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