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The roles of morphology, individuality and arrival from migration in the foraging ecology of Bar-tailed Godwits at the Manawatū River Estuary

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Abstract

Bar-tailed Godwits (*Limosa lapponica baueri*) are a hugely size-variable shorebird exhibiting reverse sexual dimorphism as well as substantial variation within the sexes. This variation is especially pronounced in bill lengths, and differences in bill size could result in dietary differences between individuals. I studied the foraging ecology of individually-marked godwits at the Manawatū River Estuary in New Zealand, a small site amenable to making repeated observations of birds by videography. Specifically, I investigated the effects of bill size variation on intake rates and diet composition of godwits and tested for individual specialisation. Birds were found to use prey-specific foraging modes, the effect of which far outstripped that of any morphological or environmental factor. I found that shorter-billed birds (males) had slightly higher and less variable intake rates than their longer-billed (female) counterparts. The shorter-billed birds focused their efforts on catching small surface prey such as *Potamopyrgus*, to the extent where around half of the males specialised on these small snails. In comparison, longer-billed birds ate a more diverse array of prey items, notably consuming more worms which were buried deeply in the sediment. In addition to some birds specialising on certain prey, other prey were taken preferentially by only certain individuals across the size spectrum. This suggests that the diets of godwits are not only influenced by morphology but also by individual preferences of the birds themselves.

I also tested for a carry-over effect of prolonged flight on foraging performance of godwits. The 8–10-day post-breeding migratory flight of godwits direct from Alaska to New Zealand is the longest known endurance flight of any land-bird. This flight has many expected physiological impacts, including a reduction in digestive tract mass that could lead to lower functionality of the digestive tract and therefore limit intake rates after arrival. By monitoring the daily occurrence of marked birds I determined when birds arrived on migration, and tested whether intake rates and diet choice changed in the fortnight after birds arrived. I found that intake rates were slightly higher and less variable with time since arrival. Furthermore, there was an increase in the consumption of the hard-shelled mud snail *Amphibola crenata* with time, suggesting a recovery of gizzard mass. Given the scale of the migration, however, these effects were surprisingly small and imply that diet choice and energy intake are affected only slightly by a physiological carry-over effect from migration.

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Chapter 1:

Review of foraging and migratory patterns of Bar-tailed Godwits

Bar-tailed Godwits (*Limosa lapponica*) exhibit among the highest degrees of sexual size dimorphism of any shorebird species. Female birds are substantially heavier and larger than males and have a disproportionately long bill when compared to males. Male bills range from 7–9 cm whereas females have bills from 9–13 cm in length (Conklin *et al.* 2011), a similar pattern of which is seen in other species to varying degrees (Moorhouse 1996; Navarro *et al.* 2009; Nebel & Thompson 2011). Because of the size difference between bills of males and females, it follows that they could have access to different prey items as is seen in other species (Ethan & Roberts 1993; Webster 1997). Whether this is the case is not yet well known in shorebirds.

Bar-tailed Godwits also undertake the longest reported uninterrupted migration of any species in the world (Battley *et al.* 2012). Adults migrate annually between their breeding grounds in Alaska and their 'wintering' grounds in New Zealand. Their southern migration to New Zealand is a non-stop, 11,500-km flight taking over 8 or 9 days. Over this time the birds utilise much of the available energy stored in their bodies and so arrive at their non-breeding grounds severely emaciated, having lost up to half their body mass (Piersma 1998). This means that upon arrival the birds' energy requirements are very high if they are to survive. The effects that migration has on the physiology and behaviour of birds have been studied extensively, but the effect that these changes specifically have on foraging have been examined less intensively and not in Bar-tailed Godwits.

The distribution of bill lengths of godwits at the Manawatū River Estuary (and in New Zealand generally) (Conklin *et al.* 2011) is bimodal, with approximately normally distributed ranges of male and female bill lengths, with little overlap between them (Figure 1). Bill morphology reflects foraging strategy in birds (Nebel *et al.* 2005), so a long bill could be presumed to be under selection pressures for probing. On their breeding grounds, godwits forage largely on surface prey as the predominant habitat is tundra, while their non-breeding habitat is largely mudflats with prey both on the surface and buried in the substrate (McCaffery & Gill Jr. 2001). Selection on the non-breeding grounds for divergent bill lengths between the sexes could occur if there was pressure to minimise competition between sexes and individuals. However, bill length also varies systematically across the Alaskan breeding range, as do body size and breeding plumage, with larger birds of both sex in the south and smaller birds in the north (Conklin *et al.* 2011). This suggests that the major selection pressures on bill length occur on the breeding grounds, or that there is selection on size in Alaska and bill covaries with size. Birds from the entire Alaskan breeding range evidently mix across all sites within New Zealand (Conklin *et al.* 2011), resulting in the spread of large and small birds within each population. This suggests that other factors drive the selection for variable bill lengths in their breeding grounds and suggests that any effects on foraging in the non-breeding grounds in New Zealand may be a by-product of this selection.

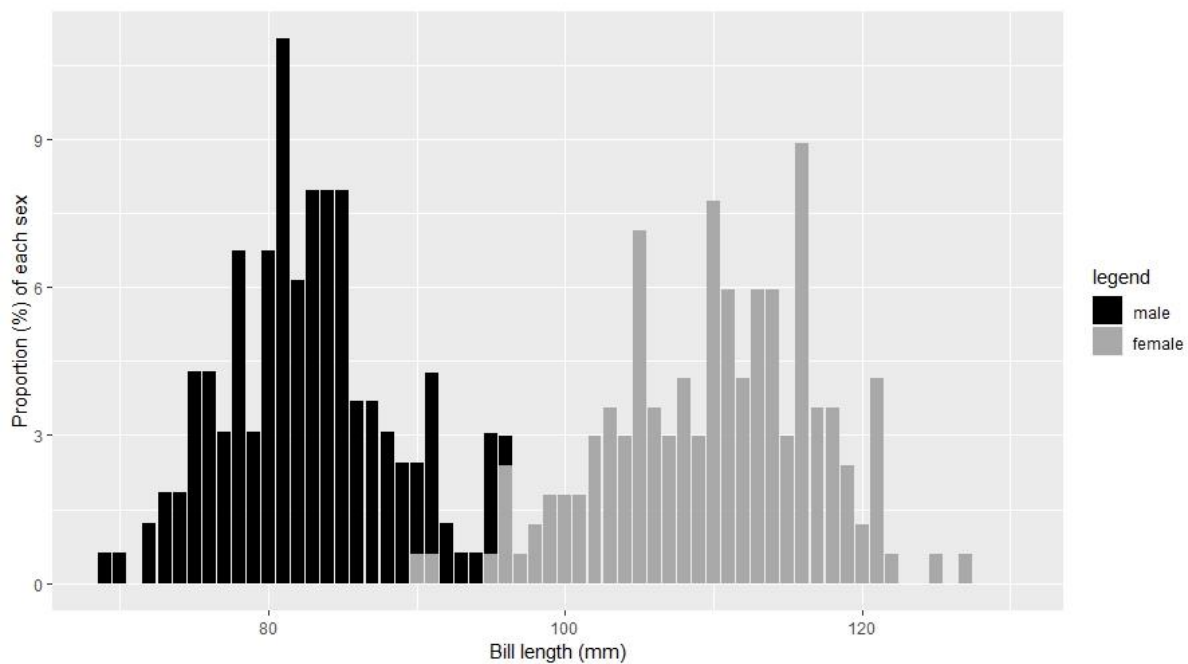


Figure 1: Bill lengths of godwits present at the Manawatū estuary, shown as a proportion of each sex represented by each length. $n = 134$ for males, 124 for females. (P.F. Battley, 2018, unpublished data).

In this chapter I review the literature relevant to the foraging ecology of godwits in New Zealand, addressing three major points:

1. What are thought to be the major drivers of sexual size dimorphism in birds?
2. What physiological and behavioural changes occur in birds during long-distance migration?
3. What are the possible effects of the above two ecological features on the foraging patterns of recently arrived migratory birds?

Sexual Size Dimorphism in birds

Difference in sizes between males and females is called sexual size dimorphism (Friedman & Remes 2016), and can be biased towards either sex. Species where females are larger are frequently termed ‘reverse sexually dimorphic’ (Brunce *et al.* 2003; Weimerskirch *et al.* 2009; Pande & Dahanukar 2012). Size differences can be minor or extreme such as in the extinct moa in New Zealand, some species of which had females up to three times the size of males, leading early taxonomists to believe they were separate species (Brunce *et al.* 2003; Olson & Turvey 2013). Size dimorphism can be reflected in body sizes, or any differences in the morphology of a sex such as a larger or different-shaped bill. The extent and direction of the dimorphism can reflect different selection pressures faced by males and females within a species (Friedman & Remes 2016). Bill size, for example, can be influenced both by natural

selection and sexual selection as bill morphology plays a role in both foraging and interactions between individuals (Olsen *et al.* 2013). Bar-tailed Godwits are known to be highly dimorphic in size. In a sample of premigratory birds sexed by dissection, females weighed 490–620 g and had bill lengths of 102–122 mm, while males weighed 370–500 g and had bill lengths of 71–97 mm (Battley & Piersma 2005b), confirming that godwits are reverse sexually dimorphic. Bar-tailed Godwits also exhibit sexual dimorphism in their breeding plumage, with males developing a far more rufous colouration than females, which develop noticeable barring on their underparts. Furthermore, there appears to be a trend for the more northern-breeding males to develop more pronounced colouration in the breeding season than their southern-breeding conspecifics. This pattern is mirrored in females, who also develop greater barring with increasing latitude (Conklin & Battley 2011; Conklin *et al.* 2011).

The causes of sexual size dimorphism are generally explained by two main hypotheses: sexual selection (Quillfeldt *et al.* 2011; Olsen *et al.* 2013) and resource partitioning (Donald *et al.* 2007; Freeman 2014). The sexual selection hypothesis suggests that differential size morphology is driven by sexual selection. This is the selective process that solely influences reproductive success in a population, regardless of the effect this has on individual survival (Jones & Ratterman 2009). Sexual selection that results in larger males suggests that males compete directly with each other. Being larger may increase the dominance rank of an individual, for example as seen in Montezuma Oropendolas (*Psarocolius montezuma*) (Webster 1997). The direction of the size dimorphism bias reflects the pressures that the sexes face. For example, in a polygynous species, males compete with one another, so a larger body or bill is advantageous to secure matings with multiple females. Conversely, in species where males engage in acrobatic aerial displays to gain mates, there is a notable reduction in the size of males in comparison to females as a smaller size allows for increased manoeuvrability (Szekely *et al.* 2000). This is particularly relevant to Bar-tailed Godwits whose males are known to engage in such displays (McCaffery & Gill Jr. 2001).

Resource partitioning is the other major driver of size dimorphism (Shine 1989). This hypothesis is founded on the premise that males and females compete with one another for resources, so a reduction in intersexual competition can benefit individuals of both sexes (Mancini *et al.* 2013). Resource partitioning can occur through behavioural differences and physical differences, leading to a debate of cause and effect. Sexually dimorphic foraging apparatus begs the question of whether different bill sizes resulted in niche partitioning, or vice versa. In some cases, resource partitioning can occur without any notable sexual size dimorphism (Freeman 2014). The degree to which size dimorphism can influence foraging will be discussed in a later section.

Moorhouse (1996) suggested that the sex exhibiting the greatest change in morphology will explain the main cause for the divergence between sexes. For example, female Huia (*Heteralocha acutirostris*) had a substantially larger, curved bill compared to the males (Frith 1997) which suggests that resource partitioning was the cause. Sexual selection acts more heavily on male traits than it does on female traits (Jones & Ratterman 2009; Hosken & House 2011) as females are frequently the limiting sex, leaving males to compete for mates. Where this is the case, if females were to be larger it would likely be for reasons pertaining to resource partitioning. However, as with any 'rule' in biology there are exceptions where males are the limiting sex, thus reversing pressures (Jones & Ratterman 2009). It may be useful to instead look at body proportions in addition to overall size.

In many cases, sexual selection does appear to be the driving factor behind sexual size dimorphism. For example, a study investigating the bill size and foraging of a pelagic seabird, the Cory's Shearwater (*Calonectric diomedea*), found that there is a notable difference in size between male and female bills. Upon examining foraging area and food intake they also found no difference between males and female foraging patterns during their breeding season (Navarro *et al.* 2009). They concluded that agonistic interactions within sexes was the likely cause rather than resource partitioning. Another example of sexual dimorphism driven by sexual selection was put forth by Olsen *et al.* (2013). This study examined bill size in Swamp Sparrows (*Melospiza georgiana*) and found that female mate choice selects for larger billed males. Similarly, Riley and Smith (1992) found no evidence of resource partitioning in Emerald Toucanets (*Aulacorhynchus prasinus*) despite the species exhibiting sexual dimorphism in bill size, as did Greer *et al.* (2015) in a study of Kea (*Nestor notabilis*).

Other studies of different species find the opposite to be true. Shorebirds exhibit a substantial degree of reverse size dimorphism, particularly in bill sizes between males and females. In many species, females have only slightly larger bodies but have a disproportionately longer bill (Nebel 2005). The predominance of exaggerated size dimorphism in bill length suggests that resource partitioning is the cause of their dimorphism (Nebel & Thompson 2011). Data for this conclusion came from a morphometric analysis of over 150 species of shorebirds and is supported by the higher degree of dimorphism in bill size as opposed to body size in these species. As is clear in Bar-tailed Godwits and other species, sexes can have markedly different morphology to one another. This difference can include extreme differences in foraging apparatus, the effects of which may differ on a case-by-case scenario. The potential effects of such sexually dimorphic foraging apparatus and the ability of birds to forage will be examined later in this review.

Changes in physiology and behaviour from migration

Migration, by definition, is the seasonal movement of animals from one area to another, often occurring twice a year. This pattern is well observed in birds, from rails and grebes to waterfowl, shorebirds and passerines (Newton & Brockie 2010), with one in five species engaging in this process (Somveille *et al.* 2015; Somveille 2016). Migratory species can exhibit short-distance or long-distance patterns of migration. Migration patterns are not necessarily consistent within a genus or even species as many exhibit flexibility; some populations of a species migrate only a short distance while others travel a greater distance (Chan 1995; O'Reilly & Wingfield 1995; Ceresa *et al.* 2016; Shamoun-Baranes *et al.* 2017). Even in Bar-tailed Godwits there is variation between populations. The subspecies *baueri* over-winters in New Zealand after migrating nonstop from Alaskan breeding grounds. This is a substantially longer total migration when compared to the Australian-wintering subspecies *menzbieri* that has a southbound migration involving stopovers in multiple locations down the east Asian coast (Battley *et al.* 2012).

The ultimate cause of migration is difficult to determine, considering the distances some species migrate (Boyle *et al.* 2011). However, it is presumed that migration increases survival rates over their wintering season. Seasonality appears to be the major ultimate cause for migration in many species of migratory birds (Boyle *et al.* 2011; Somveille *et al.* 2015), with most migrations occurring alternately between breeding and nonbreeding seasons (Myers *et al.* 1985; Newton 2011). Species' ranges can be narrow, such as that seen in Allen's Hummingbird (*Selaphorus sasin*) that winters only in a small area of central Mexico (Clark & Mitchell 2013) or wide, as is the case for Sanderlings (*Calidris alba*) where their nonbreeding range covers more than 100° latitude (Myers *et al.* 1985).

Newton (2011) outlines two main migratory patterns: obligate and facultative migrants. He suggests that obligate migrants are those that have a relatively consistent migration pattern, pre-emptively leaving prior to a seasonal scarcity of food sources. Many of these birds are long distance migrants, such as Bar-tailed Godwits and many other shorebirds. Facultative migrants do not engage in any consistent migration pattern and instead exhibit flexible timing based on food availability during the winter. Such migrations are predominantly short-distance. Even in obligate migrants, migration can be variable; sometimes a bird will delay or even forgo migration from its wintering grounds for the season. This occurs most often with first year juveniles although others can also 'over-summer' for reasons that may include non-occurrence of moult, inadequate nutrition prior to migration or other health issues (McNeil *et al.* 1994; Cooper *et al.* 2015). Juvenile Bar-tailed Godwits are a good example of this as they show delayed maturity and after their initial southbound migration, do not migrate again for another three or four years (Battley 2007).

Migration is a very strenuous undertaking for any animal and so requires numerous physiological and behavioural changes to occur. These changes can differ between and within different seasonal migrations, e.g. between spring and autumn migrations. For example, Western Sandpipers (*Calidris mauri*) migrating during late spring as opposed to early spring (both towards the breeding ground) have higher testosterone levels. Additionally, their corticosterone levels are higher in spring migration as opposed to autumn migrations (O'Reilly & Wingfield 1995). For the purposes of this study, the most important changes to migratory species are those that occur over the course of migration.

Perhaps the most notable of changes are those pertaining to body mass. Migrating birds, especially long-distance migrants, enter a form of fasting. During flight, birds do not eat and so draw all the energy they need from stored deposits built up prior to migration. Fat is the primary fuel deposit stored on the body prior to migration departure. This occurs to the extent that just prior to departure, the fat component of many migrating shorebirds such as godwits averages 30–45% of body mass (Battley & Piersma 2005b), with some even in excess of 50% of their total body mass (Jehl Jr. 1997b; Piersma & Gill 1998). This may even result in temporary flightlessness in long-distance migrants such as the Wilson's Phalarope (*Phalaropus tricolor*) (Jehl Jr. 1997b). Fat accumulation to the extent of obesity is not the only physical change to occur prior to migration. One study found that immediately prior to departure, birds appear to experience a sudden reduction in the mass of their digestive tract (Piersma & Gill 1998). A fully functional digestive tract is of little use during flight and is instead an unnecessary weight. Further studies also support atrophy of both the digestive tract and muscles not used for flight such as leg muscles (Piersma *et al.* 1999).

Over the course of migration, birds draw their energy from stored reserves (McWilliams *et al.* 2004). Migratory flight is a very high-energy undertaking requiring the constant use of muscles at high intensity, during which energy stores are catabolised. The Great Knot (*Calidris tenuirostris*) has been found to reduce their basal metabolic rate (BMR) over the duration of migratory flight (Battley *et al.* 2001). Traditionally, physiological changes occurring during migration have been studied through simulated migrations in a wind tunnel (Rothe *et al.* 1987; Lindström *et al.* 1999; Klaassen *et al.* 2000; Lindström *et al.* 2000; Jenni-Eiermann *et al.* 2002). Such studies allow direct measurements to be taken during flight that would not otherwise be possible in the wild. Data from these studies are important as they have added evidence supporting the lower metabolic rate in birds during migratory flight when compared with non-migratory flight (Klaassen *et al.* 2000). Another study on captive-raised ibis utilized a more novel approach whereby tame ibis were trained to follow an aircraft to simulate migration flight (Bairlein *et al.* 2015). This study found that longer flights had an overall lower energy expenditure than did short flights, in part because of the elevated energy demand during take-off and

climbing in altitude. This allows the birds to have greater endurance on the long flights needed for migration.

Fat deposits are the most important fuel source for a migrating bird, however it is now accepted that this is not their only energy source. When fuelling, it appears that birds also additionally store some non-fat resources (Piersma 1990; Lindström & Piersma 1993; Klaassen *et al.* 2000). In accordance with this, there appears to be evidence that muscle mass, digestive tract and other lean tissue is also catabolized at a steady rate throughout the migration process. Prior to migration, Klaassen and Biebach (1994) found that of mass gained while fuelling, up to 15% could be attributed to protein alone. Biebach (1998) and Jenni-Eiermann *et al.* (2002) found that during migratory flight, birds catabolize both fat and protein, at a ratio of approximately three to one. This was important as prior to this it was thought protein catabolism was a last resort fuel supply. Furthermore, Lindström *et al.* (2000) measured the pectoral muscle mass of Red Knots (*Calidris canutus*) and found that the speed with which the birds could consume and replace their muscle mass supports its use as a fuel source during migratory flight.

Different resources are catabolised at different rates during migratory flight. As previously mentioned, migratory flight has a lower rate of energy expenditure than non-migratory flight (Klaassen *et al.* 2000). A major part of this is the reduction in the proportion of flight spent taking off, since taking off requires more energy than any other part of flight (Rothe *et al.* 1987). This also uses a different fuel source for such high intensity activity. During initial take-off and climbing in altitude it appears that the main energy sources are from carbohydrates, after which metabolism shifts to lipid and protein fuel sources (Bairlein *et al.* 2015).

The most important physiological aspect of migration for the study following this review is the state in which the bird arrives after migration. Fat content is heavily catabolised over the course of migration. Additionally, muscle mass is also catabolised throughout flight (Biebach 1998; Lindström *et al.* 2000). This was initially surprising given that fat contributes approximately eight times the energy content per unit mass when compared to protein catabolism (Lindström & Piersma 1993). Klaassen *et al.* (2000) proposed that protein catabolism is a means to provide water during flight to prevent dehydration. Gerson and Guglielmo (2011) found that Swainson's Thrushes (*Catharus ustulatus*) flown in low humidity conditions catabolised their protein sources faster than those flown in more humid conditions, supporting the idea that protein catabolism is used to maintain water balance. The extent to which protein can be catabolised is extensive; in Garden Warblers (*Sylvia borin*), skeletal muscles such as those in the breast and legs can be reduced by 19% (Biebach 1998; Bauchinger & McWilliams 2012). The extent of this catabolism results in an extreme version of phenotypic plasticity wherein a

bird arrives from migration weighing only half what it did a few days prior when it departed (Piersma 1998). A subset of this plasticity is phenotypic flexibility wherein any changes are reversible so that a bird arriving in such an emaciated state can quickly regain body mass (Piersma & Lindström 1997). Very few organs or other tissues in the bodies of migrating birds remain homeostatic during this period of mass reduction.

Details of the reduction in mass of shorebirds during migration were recorded by Battley *et al.* (2000). In this study, Great Knots were caught just prior to and after migration and their body composition was analysed. From these birds, it was discovered that migration flight results in a reduction of all organs except for the brain and perhaps the lungs. The rate of decline of these is not constant across all tissues – fat experienced the greatest reduction but skin, intestines, liver, and salt glands among other tissues all experienced noticeable decreases. Some of this reduction in mass is understood to counteract unnecessary weight during migration. Other reductions appear to be unavoidable such as in the case of kidneys and liver where their function remains necessary during migration. As fuel sources are catabolised, less muscle is needed to support the bird during flight. Therefore, reduction in unnecessary muscle tissue provides both a further reduction in weight as well as extra catabolised energy (Pennycuik 1998).

Bauchinger and McWilliams (2012) further support these findings, showing across species that most heavily catabolised lean tissues include organs like the liver and small intestine, whereas skeletal muscle is reduced less during migration. They outline that this could be due to differences in the inherent rates of protein turnover in different organs, with the liver and small intestine experiencing the highest reductions due to their faster rates of turnover (which they referred to as the ‘protein turnover hypothesis’). These organs are also the easiest to rebuild, exhibiting substantial capacity for phenotypic flexibility. While similar studies have not yet been conducted on Bar-tailed Godwits, it appears likely that a similar pattern would be observed as they too are long-distance-migrating shorebirds. For the purposes of this review, the most important result from this study is the notable reduction in mass and potential functionality of the digestive tract, the repercussions of which will be discussed next.

Effects on foraging

Both migration and sexual size dimorphism are likely to have some impact on the foraging proficiency of a bird. Birds experience a myriad of changes in their bodies during migration, most notably major reductions in fat stores, muscle mass, and digestive tract mass (Klaassen & Biebach 1994; Biebach 1998; Battley *et al.* 2000). A reduced digestive system is expected to have lower functionality when

compared to a regular gastrointestinal tract. It follows that, post-arrival, birds would undergo a recovery period during which they recover their foraging and digestive proficiency. This pattern was observed by Klaassen and Biebach (1994), who found evidence of a recovery period in recently migrated Garden Warblers (*Sylvia borin*). Immediately after arrival, birds experienced a period of little or no mass gain as they were unable to forage at their usual rate. Possible causes of such reduced efficiency can be understood from a study of Red Knots by van Gils *et al.* (2003). This study shows how gizzard size reflects the capacity to process particular dietary items. These birds are known to forage heavily on bivalves with hard shells requiring some force to grind up in their gizzard and by manipulating the diets provided to individuals, they were able to show that individual birds can change their digestive morphology based on their predominant prey available.

A similar pattern of reduced digestive efficiency has been observed in other studies. Gannes (2002) examined the patterns of refuelling in Blackcaps (*Sylvia atricapilla*) at a stop in the Negev Desert. He found that birds stopping for more than a day initially endured a period of very little mass gain. This was followed by a very large mass gain once a stopover reached a certain time threshold of about three days. This threshold suggests there is a recovery time in which birds have reduced digestive assimilation functionality, while their organs recover (Biebach 1998). Karasov and Pinshow (2000) also examined the limitations to nutrient assimilation during post-migratory flight foraging of Blackcaps, by fasting captive held migrant birds. They found that fasted birds did not immediately achieve high rates of digestive assimilation, again supporting the existence of a post-migration recovery period. Similar studies on Bar-tailed Godwit recovery do not appear to have been conducted.

The massive reduction and reconstruction of organ tissues in migrant birds is an example of phenotypic plasticity (Piersma 1998). The digestive organs are well known to respond to changes in levels of fibre and energy density (Battley & Piersma 2005a). For instance, Brown Teal (*Anas chlorotis*) are able to modify the length of their gut depending on their food sources, with shorter guts resulting from lower fibre intake (Moore & Battley 2006). Similar plasticity in digestive organ size has been found in response to fibre intake for other species such as the Japanese Quail (*Coturnix japonica*) (Starck 1999; Starck & Rahmaan 2003). Such capacity for diet related plasticity is worth noting as this is widely observed in bird species including shorebirds (Karasov 1996). Red Knots are known to change the thickness and size of their gizzard and other digestive organs in response to prey type, for example soft shelled prey like worms as opposed to harder shelled molluscs (Piersma *et al.* 1993; van Gils *et al.* 2003; Battley & Piersma 2005a). van Gils *et al.* (2003) in particular found that knots fed on soft food items such as trout pellets had decreased gizzard mass in comparison to those fed hard-shelled prey such as mussels. Additionally, they found that birds with larger gizzards could maintain higher intake rates of shelled prey compared to their counterparts with smaller gizzards. This illustrates how

increased gizzard muscle mass is required to physically process some prey items such as bivalves or crabs, both of which are known prey items of Bar-tailed Godwits. Furthermore by swapping prey items given to the knots, they again highlighted the plasticity of individual birds who can rapidly change their gizzard mass to adequately process different prey items, a change known to occur within 6 to 8 days (Dekinga *et al.* 2001). When examining post-migration recovery periods, such relationships between gut and prey type could be considered. As a bird's gut rebuilds after migration, certain prey types could be more beneficial depending on the state of the gut at any point in time. This will need to be considered when examining the post-migration foraging behaviour of Bar-tailed Godwits.

Segregation patterns are often observed between species based on the species' different morphologies. For example, resource partitioning has been well observed between species of shorebirds foraging on the same mudflat, with different species preferring certain prey types and regions within the same ecosystem (Bocher *et al.* 2014; Lourenco *et al.* 2016) thus reducing interspecific competition. Sexual dimorphism then is an extension of such different morphologies, just on an intra-specific scale, and can lead to resource partitioning between sexes of the same species.

Size dimorphism has a direct influence on avian foraging patterns, both through altering access to prey types in addition to changing the energy requirements of each sex (Duijns *et al.* 2014). In Bar-tailed Godwits there is evidence for direct competition between male and female birds; larger females in The Netherlands have been observed to monopolize good feeding areas, pushing the males to other areas (Both *et al.* 2003). Similar distribution patterns have also been observed in Black-tailed Godwits (*Limosa limosa*) with males frequenting different regions of the mudflats than females (Catry *et al.* 2012). However, Alves *et al.* (2013) found little evidence of this large-scale spatial segregation, instead finding the major segregation was prey choice between sexes. Another study by Finn *et al.* (2008) found that both substrate resistance and prey availability were the major driving factors of the distribution of Eastern Curlews (*Numenius madagascariensis*). Coupled with the preferences of the different sexes, this would help explain sex-related differences in foraging patterns. Furthermore, Santiago-Quesada *et al.* (2009) propose that there is a difference in gut assimilation efficiency between sexes which would also influence prey and habitat choices between the sexes.

An early study by Pierre (1994) examined the foraging behaviour differences between male and female Bar-tailed Godwits in New Zealand. She found that males tended to 'tap' the mud surface more than probe it compared to the females, and that males had a higher overall feeding success. Differences in foraging proficiency can go further than studying differences between sexes and can instead determine relationships with bill length. Prey availability and preferences between males and females does appear to be related to bill size. Male and female Black-tailed Godwits choose different

prey types, possibly because they can probe to different depths. Benthos sampling has shown there to be differences in depth of invertebrate prey species within the top few cm of a mudflat (Sherfy *et al.* 2000), so it follows that different bill lengths would have access to different prey items as found in Black-tailed Godwits by Catry *et al.* (2012). There is also a large amount of intrasexual variation as well, suggesting that there is a degree of individuality between birds in terms of what prey they consume (Catry *et al.* 2014), however more research would be needed to determine how consistent this is.

Where resource partitioning is observed alongside sexual size dimorphism, there is often debate over cause and effect: did sexual dimorphism cause niche divergence, or did niche divergence cause sexual dimorphism? A comparison of sexual size dimorphism observed in both Great Bustards (*Otis tarda*) and the extinct Huia provides a good case example for either of these cause/effect scenarios (Moorhouse 1996; Bravo *et al.* 2016). Bravo *et al.* (2016) concluded that distinct sex roles and requirements drives the divergence of diet in these bustards. For the purposes of this study, the debate over the cause of sexual dimorphism will be explored no further, but any correlation between niche divergence and this sexual dimorphism will be analysed. As Bar-tailed Godwits exhibit a wide range of bill lengths both between and within sexes, they are an ideal study species of the effects of differing bill morphology on foraging behaviour. This size variation is due to selection pressures the birds face in their breeding grounds, and any spatial pattern is not maintained in their non-breeding grounds. Moreover, as all sizes are represented in the Manawatū Estuary population, and all forage within the same habitat, studies of feeding behaviour should be able to discern whether these differences influence foraging patterns based on variability of morphology.

Aim of thesis

The aim of this thesis is to examine heterogeneity in the foraging behaviour of godwits. Based on the sexual dimorphism in the species, I examine the factors influencing their foraging behaviour including bill length and individuality of the birds. I also test whether there is a carry-over effect of migration on foraging behaviour and intake rates in the days immediately after arrival.

Thesis study species and location

The study species for this thesis is the Bar-tailed Godwit (*Limosa lapponica baueri*), which occurs on mostly soft-shore intertidal environments around New Zealand, across both the North and South Islands (Heather & Robertson 2005). They are largely carnivorous, and generally prey on polychaete worms, crabs and other invertebrates living in the sediment (Duijns *et al.* 2013; Lourenco *et al.* 2016). They are active foragers, feeding on mudflats even if covered by up to 15 cm of water. They are known

to probe in the mud or use a rapid sewing-machine movement to capture prey (Higgins & Davies 1996). Choi *et al.* (2017) studied prey intakes of Bar-tailed Godwits on migration in China, and found that while they selected for polychaete worms, the birds' primary source of biomass intake was from bivalves. At the Manawatū River estuary, birds have been observed to also consume large mud snails and shellfish siphons. Analysing their diet is frequently done by collecting faecal matter, however Lourenco *et al.* (2016) also used digital videography to analyse foraging behaviour and intake rates of shorebirds.

A small population of approximately 200 birds frequents the Manawatū River Estuary every year where they 'over-winter' through the New Zealand summer on a small area of mudflats, approximately 20 ha in total. The adults arrive from Alaska through September and into October and remain until migrating north in March, while some immature birds stay at the site through the northern breeding season. The local population has been extensively studied and monitored at the Manawatū Estuary since 2006 (Battley & Piersma 2005b; Battley & Conklin 2010; Battley *et al.* 2011; Conklin & Battley 2011; Conklin *et al.* 2011; Conklin *et al.* 2016). This monitoring included a banding programme using both colour bands and engraved leg flags that has resulted in a sizeable database being accrued over time with biometric data recorded for every bird banded. Because of this programme, the migratory habits of individuals are known and individuals can be identified. The accessibility and proximity of this population to Palmerston North and Massey University makes it an ideal shorebird study population.

General methods

Benthos sampling was undertaken to determine size-mass relationships of prey items for biomass intake estimates from videography. This process was conducted twice, at the start of September and the end of October 2017. The estuary mudflats have been sampled many times previously so already had a pre-existing grid of GPS logged sample sites (Figure 2). Sampling consisted of 30 cm deep core samples at 40 sites across the flats, and an additional capture of mud snails and flounders to ascertain their masses. All prey items were either frozen or initially placed in 5% formalin to euthanase them, then preserved in ethanol for later sorting in the lab. In the lab they were sorted by species and size, dried at 75°C for 4 days (longer for bivalves), then ashed at 600°C. From this process, the ash-free dry mass (AFDM) could be determined and this was the measure of biomass used in subsequent estimates of intake rates for the godwits.

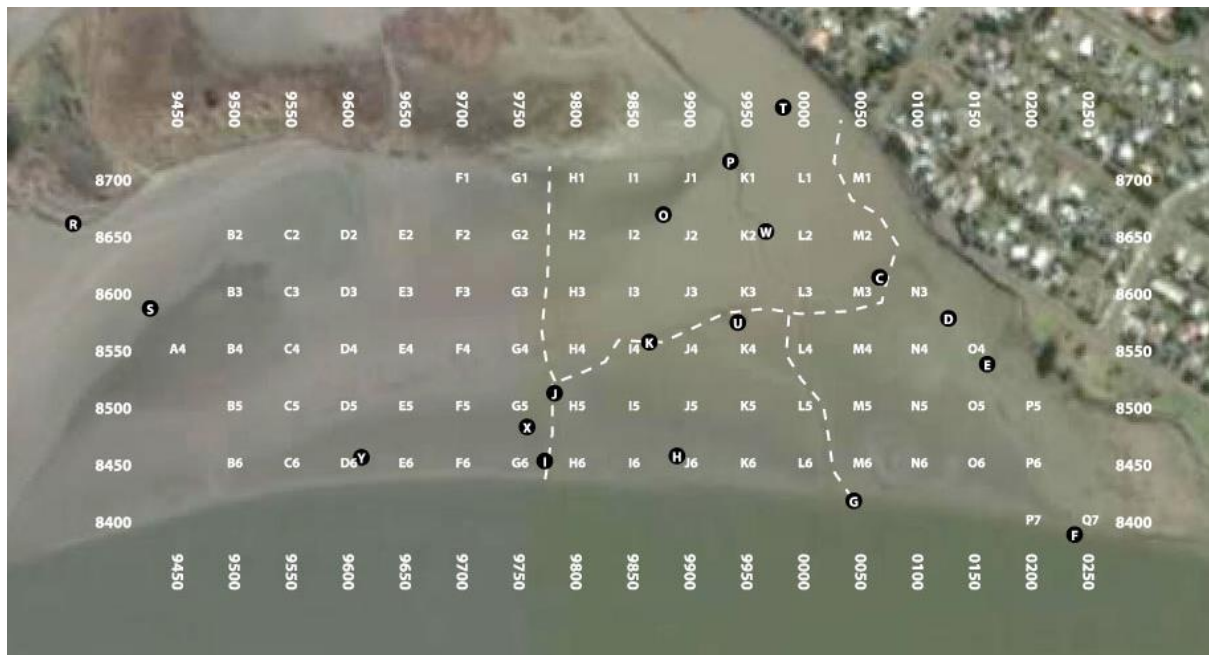


Figure 2: Grid of sample sites across the Manawatū Estuary. Grid lines are spaced 100 m apart from each other and are recorded as GPS coordinates.

Videography data were collected for both research questions at the same time. All videography was conducted at a distance from the birds and so required no animal ethics approval to record observations. Videography occurred by digiscoping with a Panasonic Lumix DMC-TS5 waterproof camera attached to the eyepiece of a Nikon EDG 85 VR Fieldscope or a Swarovski ATS80HD scope, both of which had 20–60 x lenses (Figure 3). The vibration reduction function on the Nikon scope was particularly valuable for video recording as it stabilised the image in the windy conditions on the mudflats. This allowed me to video birds from up to 100 m away without disturbing them. In addition, daily bird lists (colour-band and engraved flag combinations) were made as not all birds were videoed daily, and some were not videoed on their day of arrival. By combining the lists of birds videoed with birds seen every day, it was possible to determine when birds first arrived and thus the days relative to arrival on which they were videoed. Between the 4th of September and 26th of October 2017 I recorded just under 1000 videos of 63 individually marked birds as they foraged. Through a selective process wherein birds were weighted based on the number of days they were filmed within the first two weeks after arrival, and ensuring an even spread of bill length variation, I derived a core set of 215 videos of 34 individual birds. The initial selection process required birds to be videoed within the first 2 days since arrival. Birds that were not videoed so close to arrival were not considered for the study. The greatest weight per video was allocated to those recorded on the day of arrival and within the subsequent week, and such a process resulted in 2 to 11 videos of each bird being selected (Appendix 1). Following this, an ethogram (Table 1) was set up containing all behaviours observed in

videos that allowed all actions within the videos to be recorded for analysis, generally at a half speed in playback to ensure no behaviours were missed.



Figure 3: Nikon scope and camera mount setup for use in the field.

Table 1: Ethogram of godwit behaviours. Modifiers applied to the behaviours swallow and fail, and denoted which prey item was involved. ‘Small unknowns’ were later assumed to be *Potamopyrgus*, and ‘unknown worm’ was similarly treated with an average biomass value from fractions of worms obtained during benthos sampling.

Type	Keystroke	Behaviour	Modifiers
Point	Q	Step	Potamopyrgus
State	P	Out of view	Large Snail
State	Z	Surface Dabbling	Small worm
State	B	Handle	Medium worm
State	M	Sewing Motion	Large worm
Point	A	Peck	Crab
Point	S	Swallow	Bivalve
Point	F	Fail	Siphon
Point	J	Full probe	Flounder
Point	K	2/3 probe	Small unknown
Point	L	1/3 probe	Unknown worm
State	1	Foraging	
State	2	Non-foraging	

As the video monitoring was purely observational and focused on previously-marked birds, no Animal Ethics approval was required. Benthos sampling (which included crabs and *Rhombosolea* sp. flounder) was covered under Massey University Animal Ethics approval 17/58.

Thesis plan

Chapter 2: Heterogeneity in foraging behaviour of Bar-tailed Godwits reflects both morphology and individual preference

Many species exhibit variation in bill morphology between males and females and such is the case with Bar-tailed Godwits. There are notable differences both between and within sexes which has the potential to create diet disparities between the sexes and individuals. Longer-billed birds are likely able to access a greater range of prey than their shorter-billed conspecifics. This chapter aims to determine any differences between godwits based on their bill lengths and determine whether there is a role of individuality influencing diet choice and foraging style. Both videography of foraging godwits and benthos sampling were used for this. Benthos data allowed biomass intakes to be estimated from videos (rather than just numerical intakes). This information allowed me to determine relationships between morphology and individuality on the foraging patterns of godwits.

Chapter 3: Carry-over effects of trans-Pacific migration on intake rates of Bar-tailed Godwits are small

Chapter 3 uses the same data as in Chapter 2 but specifically addresses the effect of time since arrival in the foraging behaviour of godwits. Bar-tailed Godwits are extreme long-distance migrants, and this is anticipated to impact on their physiology via a drastically reduced gastrointestinal tract mass. Changes in physiology such as these are known to be particularly rapid, however little is known about exactly how birds respond behaviourally during the period of recovery following migration. Previous studies have suggested there may be some limitation to assimilation of nutrients for a recovering bird, but this has not been studied in relation to recovery from endurance flights. This chapter seeks to determine whether physiological recovery from migration has any impact on the foraging patterns of these birds, such as preferred foraging mode, prey selection and intake rates.

Chapter 4: General Discussion

Following the previous two chapters, this chapter summarises the main findings of these studies. It concludes with suggestions for further research.

Chapter 2:

Heterogeneity in foraging behaviour of Bar-tailed Godwits reflects both morphology and individual preference

Abstract

Foraging behaviour of birds is known to be influenced by a range of features including internal factors such as sex, bill morphology and individual preferences, and external environmental factors such as stage of tide in coastal foraging species. In highly size-variable species, bill morphology has the potential to play a major role in shaping the foraging behaviour of individuals. The Bar-tailed Godwit (*Limosa lapponica baueri*) is a large shorebird with sexual dimorphism in bill length (females are larger) and also considerable variation between individuals of both sexes. Given that bill length can limit access to buried intertidal prey, differences in bill length between individuals and between sexes may shape individual foraging behaviour and lead to systematic differences in diet between birds of different size. Additionally, preferences may exist that are unrelated to morphology but also affect how birds forage and use resources in a common environment. I studied the diet and energy intake of individually marked godwits at a small estuary in New Zealand, where birds of known bill length could be observed repeatedly on different days. I used videography and benthic sampling to describe the diet and biomass intake rates of 34 birds that spanned the size range in the local population, on 2–11 occasions per bird. Using a range of mixed models and ordination, I investigated how intake rates and diet composition varied with sex, size, behaviour and stage of tide. A role of sex or size was found, with males having slightly higher intake rates and being less variable than females, shorter-billed birds (males) favouring small, surface-dwelling prey such as the small mud snail *Potamopyrgus*, and longer-billed birds (females) taking deeply-buried worms. Furthermore, prey were captured by birds feeding with quite specific foraging modes, and foraging mode had a much greater influence on intake rates than bill or any of the measured environmental factors. Individual specialisation was evident, with almost half the males specialising on *Potamopyrgus* while one female specialised on polychaete worms. Other prey were taken non-randomly by certain individuals. Together, my results indicate that the foraging behaviour of godwits reflects elements of (fixed) morphology and individual preference. Specifically, the length of the bill affects the general choice of foraging behaviour, target prey and associated probing depth, but individuals may additionally specialise on certain prey or include certain prey types in their diet. Hence, sexual differences in morphology that are probably driven principally by selection on the breeding grounds in the northern hemisphere can contribute to dietary segregation on the non-breeding grounds in the southern hemisphere.

Introduction

Foraging behaviour contributes directly to the survival of an animal, and foraging patterns can vary both between and within species. Individual specialization, wherein birds of the same species differ in their foraging patterns from one another, can occur even in supposedly generalist species.

Morphological differences between individuals can drive this variation (Gustafsson 1988), but this is not always the case because birds with no distinctly different morphology can also favour different behaviours (Lewis *et al.* 2002). Lewis *et al.* (2002) found that these differences can occur based on sex, but also on an individual basis where observed variation is left unaccounted for by physical differences between individuals. An important way to discern any effect of individuality is to study the consistency of behaviours between foraging bouts of an individual (Woo *et al.* 2008; Milligan *et al.* 2017), as this can identify both generalists and specialists within a population. Furthermore, foraging patterns of some individuals may be consistent whereas others may be far more flexible and variable (Potier *et al.* 2015; Maynard & Ronconi 2018). Variation in foraging that cannot be explained by physical characteristics of a bird (e.g. age, sex, morphology) may be the result of individual specialization (Ingram *et al.* 2018). The array of factors that may influence the foraging behaviour of individuals highlights the complexity of a species' foraging ecology, and thus the need to distinguish between morphology-driven effects and those reflecting individuality.

Bill morphology is just one of the morphological factors that influences the foraging ecology of a species and it is indicative of different foraging niches of bird species (Forstmeier & Keßler 2001; Nebel *et al.* 2005). This is not just limited to interspecific differences, as many species exhibit significant variation between the sexes in terms of bill morphology, known as sexual size dimorphism (SSD) and this can be indicative of different foraging subniches within the species (Selander 1966). One of the major hypotheses regarding the evolution of such differences is the resource partitioning hypothesis (Nebel & Thompson 2011), which suggests that SSD has evolved as a means by which the sexes avoid competition with one another, as some studies have argued that there is observable competition between sexes (Both *et al.* 2003). However, other studies suggest that the major driving factor for SSD is sexual selection rather than niche differentiation (Szekely *et al.* 2000). Thus, there is debate over whether different foraging behaviours drove the evolution of SSD or whether the different behaviours are simply consequences of size differences driven by other selection pressures (Blanckenhorn 2005).

Shorebirds (order Charadriiformes) exhibit some of the most pronounced sexual size dimorphism in birds. Within the family Scolopacidae, reversed sexual size dimorphism is the general pattern, with females being larger than males (Cramp 1983), but there can additionally be considerable variation within the sexes. The Bar-tailed Godwit (*Limosa lapponica*) is a prime example of this. In the Alaskan-breeding subspecies that 'winters' in New Zealand and Australia (*L. l. baueri*), there is little overlap in bill length measurements between males and females, with male bill lengths ranging from c. 69–99 mm and female bills from c. 90–129 mm (Conklin *et al.* 2011). As the range of bill lengths within each

sex is as large as the difference between sexes in many species, there is the clear potential in godwits for bill lengths to create differential foraging opportunities both between and within the sexes.

Studies suggest that godwits prefer prey items such as polychaete worms (Duijns *et al.* 2013) over bulkier prey items such as bivalves, but are known to eat large quantities of bivalves on staging sites where they are the predominant prey type (Choi *et al.* 2017). Bar-tailed Godwits forage at a range of depths, from crabs on the surface (Zharikov & Skilleter 2002) to deeper burrowing worms (Esselink & Zwarts 1989). These depth disparities suggest that, due to their shorter bills, male birds may not be able to access the same prey as females (van de Kam *et al.* 2004). The larger females may potentially have higher energy requirements than their male counterparts, driving them to access different prey items to meet their requirements (Alves *et al.* 2013).

Additionally, individual specialisation could create variation in the foraging patterns of godwits. Individual variation is a factor less often accounted for in many studies and is defined by Ingram *et al.* (2018) as the occurrence of an individual utilizing only part of the overall resources available to the species, irrespective of factors such as age or sex. Durell (2000) argued that most variation can be attributed to bill morphology, but also that variation in individual skill can play a role in determining why some individuals appear to prefer certain prey types. Studies such as those by Catry *et al.* (2014) and Woo *et al.* (2008) highlight the effects of individual specialisation resulting in both specialist and generalist individuals within the population, providing a clear example of the extent of individuality in foraging behaviours.

In this study, I test the degree to which the foraging behaviour, diet and intake rates of individual Bar-tailed Godwits are affected by morphology (bill length and associated differences in probing depth) and ask whether there is evidence for additional individual specialisation that is not related to morphology. As all birds were studied on the same small open mudflat, opportunities for foraging are similar for all birds and any differences in diet and intake rate should reflect morphology and active foraging decisions rather than habitat differences.

Methods

Site details

Godwits were studied at the Manawatū River Estuary in the North Island of New Zealand (40°28'30" S, 175°14'30" E). These mudflats cover approximately 20 ha and are situated on the north shore of the estuary near the town of Foxton Beach. They are a recognised RAMSAR site as of 2005 (Manawatū Estuary Trust 2010) and provide non-breeding habitat to a small population of around 200 godwits each year.

Benthos Data Collection

Benthic sampling was undertaken from 4–7 September and 27–28 October 2017. At each time, 40 core samples of 10.5 cm diameter (area 0.0079 m²) and c. 30 cm deep were taken at evenly-spaced intervals across the mudflat on the northern side of the estuary and located via GPS (accuracy \pm 2–3 m). The upper few centimetres of the core could generally be sieved through a 1-mm sieve, but the deeper parts of the core consisted of stickier mud that had to be carefully broken apart by hand and invertebrates (mostly polychaete worms) located and removed. Invertebrates were either preserved in 5% formalin and later transferred to ethanol, or frozen (in the case of larger bivalves) before analysis. Six small flounder (*Rhombosolea* sp.) and 30 crabs (likely *Austrohelice crassa*) were caught by hand to augment the formal samples to help determine biomass values. These flounder and crabs were measured, euthanased by crushing, and either stored in formalin or were frozen.

All intact invertebrates were identified to major taxonomic group, measured, and then, either singly or in groups with others in the same size class, dried at 75°C for 48 hours or more (longer for large shellfish), cooled in a desiccator, weighed, ashed at 600°C for 6 hours then allowed to cool before being reweighed (Duijns *et al.* 2013). The individual or average ash-free dry mass (AFDM) was calculated per length for each taxon size class and used in regressions to allow estimation of biomass intake rates of godwits for different sizes of different prey. The predictive relationships between length and biomass are given in Appendix 2.

Videography

Individually-marked godwits (with colour bands or an engraved leg flag) were digiscoped (using a Panasonic Lumix DMC-TS5 camera, frame rate 30 fps, attached to a Nikon EDG VR 85 scope or a Swarovski ATS80HD scope, both with 20–60 x lenses) while foraging over the low tide periods between 4 September and 26 October 2017. Videoing occurred as outlined in Chapter 1 and lists of birds seen and videoed were recorded daily and the nearest GPS site was recorded for each video. In total, 938 videos were recorded, a selection of which were chosen for later analysis, a process also described in Chapter 1 (page 14). This resulted in a core set of 215 videos of 34 birds, where one video per day was analysed. The average length of the videos was 141 seconds (s.d. 20.79 seconds), with an average of just over six videos per bird.

Data Processing and Analysis

Processing of videos was carried out using the programme Behavioural Observation Research Interactive Software (BORIS: <http://www.boris.unito.it>), which first required an ethogram of all possible behaviours displayed. Behaviours were then recorded, including paces, relative depth of the probes (0, $\frac{1}{3}$, $\frac{2}{3}$ and full bill length, subsequently translated into actual depth based on the bird's bill

length) and the type of prey whenever visible. In some cases prey were not easily visible or identifiable from the videos and assumptions had to be made based on the bird's behaviour when retrieving prey. For example, anything very small on the surface could safely be assumed to be a *Potamopyrgus* snail as the benthos sampling found that the two most common taxa found on the surface were *Potamopyrgus* or amphipods, the former being the most visible of the two (T. A. Ross, unpub. data). The biomass of *Potamopyrgus* was averaged across all those that were gathered from sampling and assigned a single biomass value. If amphipods were consumed during videoed foraging bouts, they were undetectable. Deeper probes were assumed to be unknown worms and were assigned a single biomass value later, calculated from an average of all partial worm fragments.

During video analysis, the videos were slowed down to half speed to allow each behaviour to be recorded without having to replay the video more than twice. During the first playback, paces and foraging/non-foraging phases were recorded. During the second playback, all foraging activities of the birds, including actions and foraging states were recorded. Three foraging states were identified in the videos (visual, tactile, dabbling) and were then also incorporated as behavioural states. These three states are an extension of the known visual or tactile foraging utilized by godwits (Young 1989). Visually foraging birds walked fast and probed intermittently as they saw potential prey items. Dabbling birds would wander around hunting prey items with their bill, continually disturbing the mud's surface, and visually chasing anything they stirred up. Sewing involved repeated pecking and probing of the mud without lifting their head much. These types of foraging could differ based on the prey preference of a bird as different prey items have different behaviours, e.g. a worm buried in the mud or a snail sitting on the surface. Because of this, these states were noted in BORIS and behaviours within each were recorded. Following completion of each video, any identifiable prey items were recorded in freeze-frames based on the best visible frame from the video.

Behavioural data from each video were exported as Excel files, into which were added individual prey size estimates taken from frames of the video and processed in the software GIMP 2 (<https://www.gimp.org/>). Size was analysed by measuring, in pixels, the size of the prey item and also the length of the bird's bill. Prey size was estimated as the calculated proportion of the focal bird's actual bill length. Individual pacing rates for each video were calculated per video and later added into a master data file along with the time spent in each of the foraging states, allowing proportions of time spent in each state to be recorded. Previous studies of foraging behaviour of godwits have examined a range of aspects including searching speed, intake rate, type and sizes of prey, and the number or depth of probes (Puttick 1981; Moreira 1994), so all of these were also calculated per video to fully record all foraging behaviours.

Total biomass intake rates (g AFDM min⁻¹) (Goss-Custard *et al.* 2006) were calculated per bird based on all prey items taken in the video. This was calculated by combining the AFDM of each individual prey item consumed in the video, which were themselves estimated from their size based on the relationships between size and mass of each prey type (shown in Appendix 2), apart from *Potamopyrgus* for which the average mass was used for each individual. An average AFDM value was also used for worm fragments obtained from deep probes, calculated from fragments of worms measured during benthos sampling. In addition, the final dataset used for analysis included, for each video, the following variables: bird, sex, bill (mm), date, time relative to low tide (minutes before and after), proportion of time spent in each foraging mode (visual /dabbling/sewing), total searching speed (paces/sec), average depth probed (mm), number of probes of each depth, number of prey items taken, intake rates per prey type (g AFDM min⁻¹), and proportion of total intake that was each prey type. This dataset included 8655 probing events and 5444 individual prey captures. A range of descriptive tests were used to provide an initial picture of behaviour patterns. The pacing rate of each foraging mode was analysed with an ANOVA followed by a Tukey post-hoc test, to determine differences in the speed at which birds moved while in each mode. Following this another ANOVA with another Tukey post-hoc test was run to determine the differences in depth at which each prey type was captured, and finally a linear regression was run to analyse the relationship between average depth to which a bird probed and their bill lengths.

Factors affecting the total intake rate were analysed using hierarchical generalized linear mixed models in the R package hglm (Ronnegard *et al.* 2010). As sex, bill length and average depth probed are related (sex and bill are confounded in the sample as all birds with bills ≤92 mm were male and all with bills ≥ 95 mm were female; bill length and depth probed were related as longer-billed birds can probe deeper than shorter-billed birds), I ran models exclusively with bill, sex or average depth and compared the models to each other. These models contained two parts, the first providing information on trends of intake rates, and the second ‘dispersion’ model providing information on the changes in variance of intake rates.

Following this, dietary information was then broken down into constituent prey types. This analysis was complicated by being heavily inflated with zeros, as during most foraging bouts birds only took a subset of the prey items. Proportion data were analysed first using a Dirichlet regression from the R package DirichletReg (Maier 2014; Maier 2015), to determine any differences in proportion of prey types in relation to sex and bill length. This method averaged the data of all videos per bird, resulting in an effective sample size of 34. From this, a zero-one inflated model was run to further break down the proportion data, using the R packages rstan and brms (Bürkner 2017; Stan Development Team

2018). Zero-one inflated models are particularly useful for proportion data as in many videos birds only took one prey item and none of the others, producing a prevalence of zeros and ones in the data (Abdel-Karim 2017). This also provides information on birds that specialized on consuming one specific type of prey.

A non-metric multi-dimensional ordination plot was then used to display the relative dietary composition of the focal bird within each video using the R package *vegan* (Oksanen 2018; Oksanen *et al.* 2018). The purpose of this was two-fold, as it provides a good overview of diet diversity with regard to sex and highlights the specialists in the population. These were determined by calculating ellipses for each individual bird showing their diet composition. Specialist ellipses had areas below 0.1 units, intermediate individuals between 0.1 and 0.4 units, and generalists had areas greater than 0.4 units. In these analyses, intermediate and generalist birds were combined. The overall intake rates of these specialists were then compared with those of generalists using an ANOVA, to determine if one group maintained a higher intake rate than the other.

Intake data of each prey type were then analysed using log-normal hurdle models that have two parts, the first of which models the overall trends in the intake rate. The second of these provides the 'hurdle' estimates that model the likelihood that the intake rate of the particular prey item is 0. These are useful as they are capable of dealing with data heavily populated with 0s, and addressing the 'hurdle' between a zero intake rate and a non-zero intake rate (Ma *et al.* 2015). Three models were run for each prey type, all of which included bill, average depth of probes, time relative to low tide, and bird as a random effect. Each of the three models included one of the three foraging mode proportions. These models were then compared using Bayes Factors (Jarosz & Wiley 2014), and then run an additional two times alternating the use of either bill or average depth rather than both as these are known to be confounded variables. These were then compared again, and the best of these models was selected, thus highlighting the general trends within the intake rate data. The model was run one last time with sex instead of either bill or average depth to determine if the inclusion of sex explained the data any better than those models, as there is evidence of monomorphic species exhibiting foraging variation between sexes without a morphological explanation (Lewis *et al.* 2002). Significance of factors in these models is determined when the 95% confidence intervals generated by the model exclude zero.

Finally, consumption of some less-frequently taken prey items appeared to be specific to some individuals. An additional binomial generalized linear model (GLM) was run to analyse the likelihood that a prey item was taken during a foraging bout. Whether a prey type was consumed in a video or not was recorded as a 1 or 0 and then combined per bird. These models then compared the number

of foraging bouts in which a prey type was observed to be eaten, with the total number of foraging bouts recorded per bird while taking into account morphological traits of the bird such as sex and/or bill. This was followed by an examination of the overdispersion of the models which shows whether there is greater variation than accounted for by the model, thus acting as an indicator of non-random preference for prey types across the birds. Since no males took siphons, the model of intake rates for this prey item examined females only, thus removing sex as a variable.

Results

Foraging modes and prey types

The three foraging modes had distinctively different pacing rates, with sewing being the slowest and visual being the fastest (Figure 1; ANOVA, $F_{2,349}=144.5$, $p<0.001$; a Tukey post-hoc test supported all three modes being different).

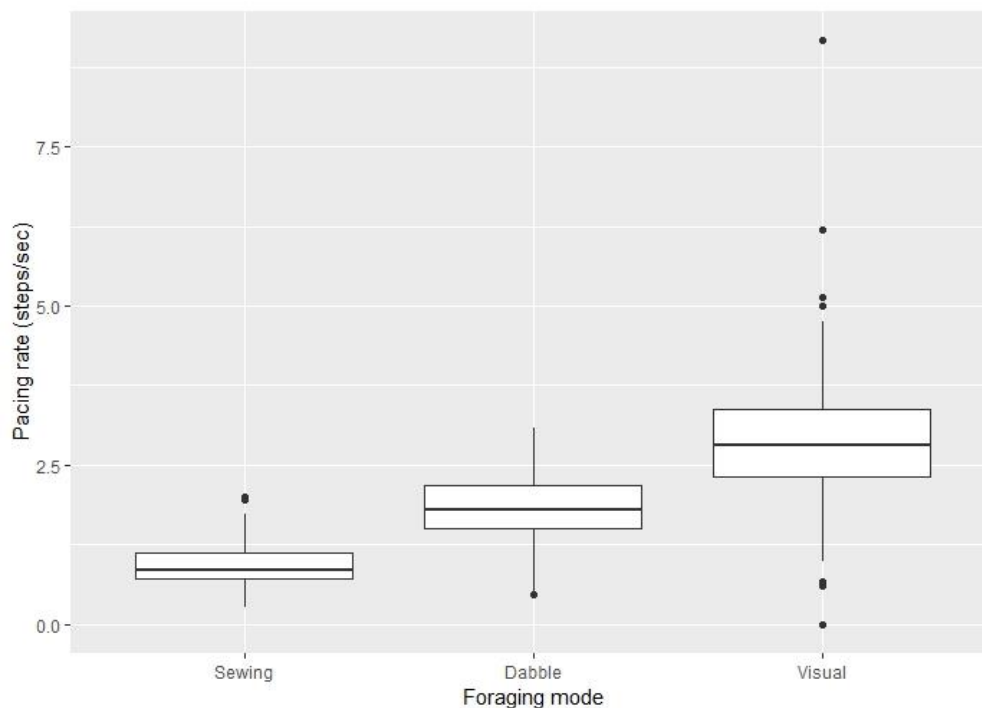


Figure 1: Pacing rates of each foraging mode. N= 63 for sewing, 119 for dabbling, 170 for visual. The pacing rate indicates the speed at which a bird is searching the mudflats for prey.

Seven major prey types were consumed: *Potamopyrgus* (assumed to be an average size of approximately 4 mm and too small to be accurately measured from videos) , *Amphibola* mud snails (average 10 ± 3 mm, range 4–19 mm), polychaete worms (*Nereis* sp.; average 53 ± 26 mm, range 13–123 mm), juvenile flounder (*Rhombosolea* sp.; average 19 ± 5 mm, range 10–35 mm), crabs (species could not be identified from the videos; average 12 ± 3 mm, range 5–19 mm), and *Cyclomactra* sp. bivalves both whole (average 21 ± 7 mm, range 11–38 mm) or just their siphons (average 18 ± 8 mm,

range 8–35 mm). There were large differences in the depths at which prey were obtained (Figure 2). Crabs, flounder and mud snails were all taken largely at the surface (except for two flounder for which the bird probed far deeper than is necessary for a surface prey item), whereas bivalves, worms and shellfish siphons were taken at depth (ANOVA, $F_{6,5437}=463.5$, $p < 0.001$). Foraging actions that captured the small snail *Potamopyrgus* were often at medium depth, despite the prey being found largely near the mud surface. A Tukey post-hoc test indicated that depths that crabs, flounder and *Amphibola* were obtained at did not differ, nor did *Cyclomactra* and worms. *Potamopyrgus* and siphons each differed from the other two groups.

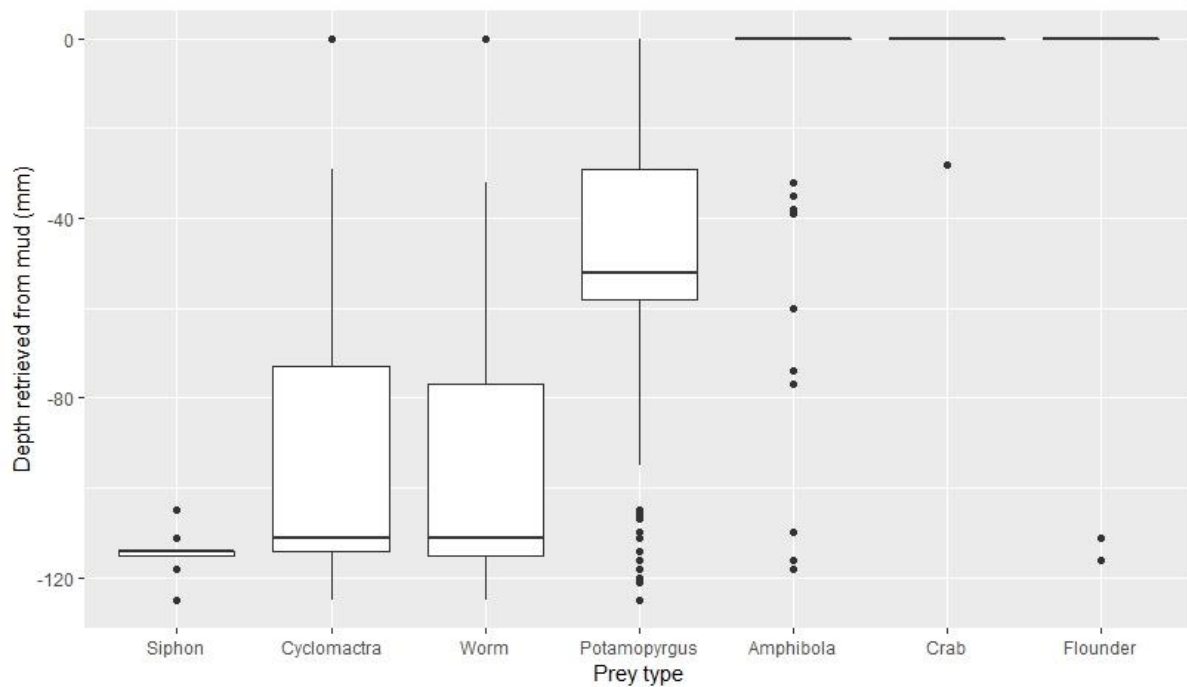


Figure 2: Depths at which prey were obtained. Depth values are combined across all birds' foraging activities. N= 21 for siphons, 82 for *Cyclomactra*, 397 for worms, 4635 for *Potamopyrgus*, 163 for *Amphibola*, 51 for crabs and 95 for flounders. Depths are shown as negative values as they are below the mud's surface.

Longer-billed individuals were capable of probing deeper than shorter-billed individuals, but there was also a tendency for the long-billed individuals (i.e. females, bill length ≥ 95 mm) to probe to full bill length frequently, whereas shorter-billed birds (males) did so infrequently (Figure 3). Consequently, averaged probing depth was positively related to bill length as shown by a linear regression (Estimate: 1.0487, $p < 0.0001$) and deeply buried prey were taken principally by females while males took prey mostly from the upper 6 cm of the sediment. Additionally, a clear difference between the preferred foraging modes of males and females was observed, as males preferred to sew while the females preferred visual foraging (Figure 4).

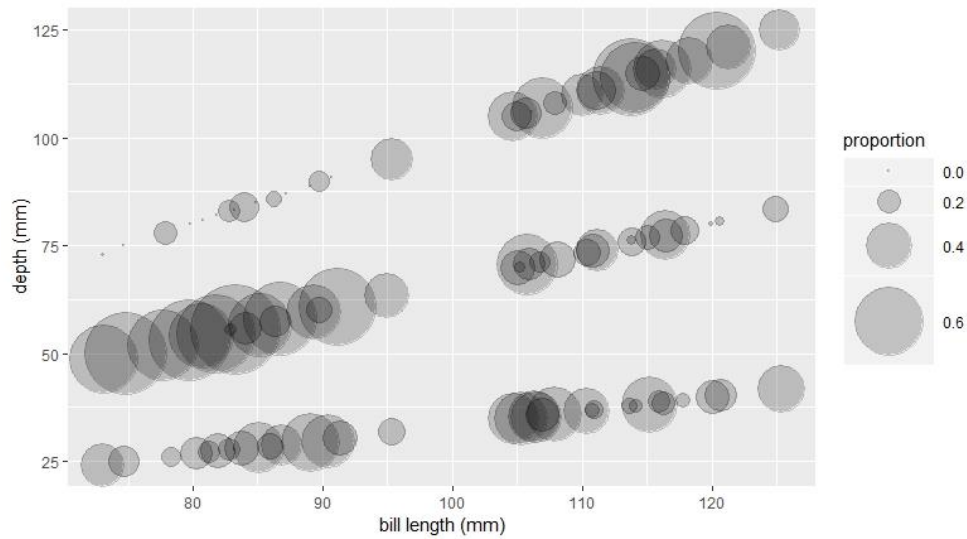


Figure 3: Depths probed to by individuals of different bill lengths, based on 8655 probes. Depths were estimated by thirds of actual bill length, hence the three depth values per bird.

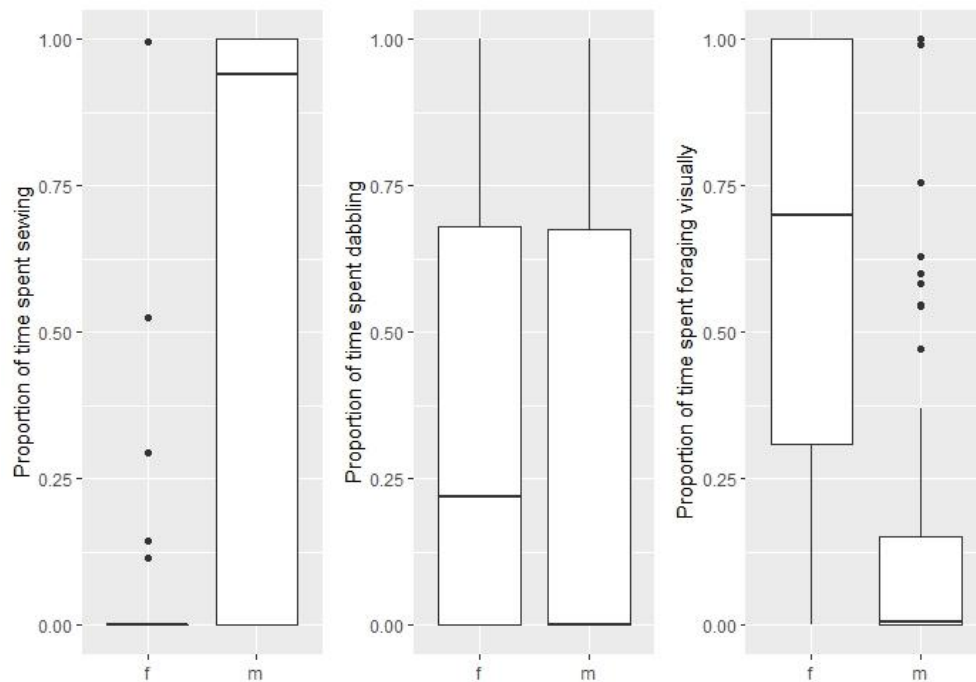


Figure 4: Proportions of time birds spent using each foraging mode based on sex. f = female, m = male, n=215 for each mode.

Effects on total intake rates

Using a hierarchical generalized linear mixed model, male birds were found to have higher intake rates than female birds and were less variable in their total intake rates (Estimate: 0.4493, $p=0.0042$; Dispersion effect: -1.4178). When the model was run using bill length instead of sex, the equivalent

pattern was found, suggesting that longer billed birds were overall less successful at foraging but were more variable (Estimate -0.015, $p=0.008$; Dispersion effect: 0.0436).

Composition of diet

Despite only minor trends in the overall intake rates, dietary composition differed markedly between individuals (Figure 5, upper). Dirichlet regressions of proportions of total intake suggest that only two prey items varied with bill length or between sexes. The proportion of *Potamopyrgus* in the diet decreased with bill length (Estimate: -0.06733, $p<0.0001$), whereas worms made up a larger proportion of the diet of longer-billed birds (Estimate 0.03923, $p=0.0029$). This same pattern held true between the sexes, with males eating more *Potamopyrgus* (Estimate: 2.1831, $p<0.0001$) but less worms than females (Estimate: -1.0235, $p=0.017$). The lower panel in Figure 5, however, shows a different pattern, with worms featuring less in terms of actual intake rate of longer-billed birds, which will be explored later.

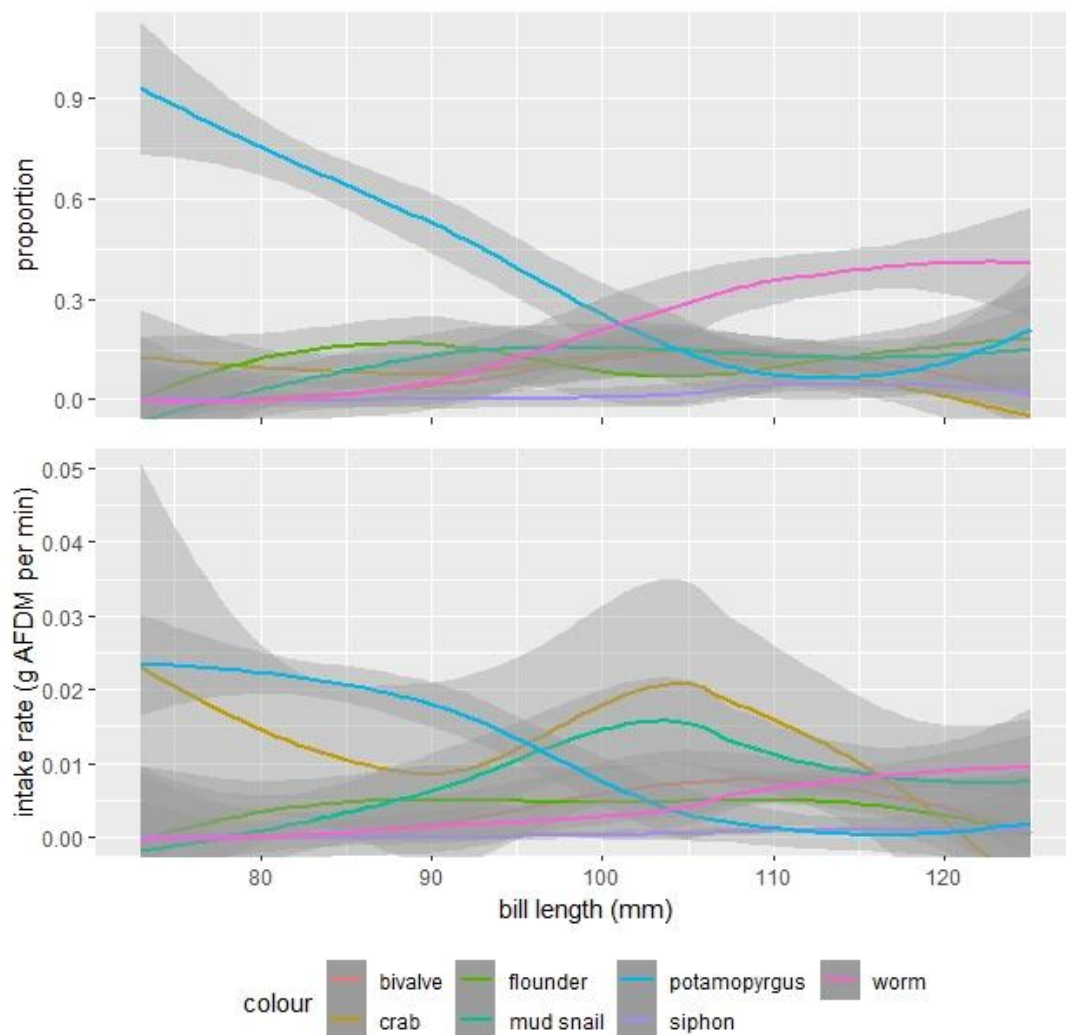


Figure 5: Smoothed proportions of diet composition and intake rates of each component. Note, no birds had bill length between 95 mm and 105 mm, so this crossover area as shown above is estimated. The smallest female bill was 95 mm, and the largest male was 91 mm.

Zero-one inflated beta models were run on both *Potamopyrgus* and worm proportions. Short-billed birds (males) were more likely to eat entirely *Potamopyrgus* than their longer-billed (female) conspecifics (shown by the negative estimates of both *zoi* and *coi* in Table 1), however of those that did not specialize there appeared to be little trend relating to bill length (shown by the bill 95% C.I. overlapping zero). Shorter-billed birds were less likely to specialize entirely on worms and were far more likely to consume no worms at all when compared to longer-billed birds, who generally ate more worms than the shorter-billed individuals (Table 1).

The NMDS ordination plot showed the relative dietary composition of each observation (Figure 6, upper), and based on all intake rates revealed a considerable difference overall in the distribution of values for females and for males (Figure 6, lower). Males were restricted to the left-hand side of the plot, with a strong cluster low on the NMDS2 axis that corresponds to intakes of *Potamopyrgus*. Females had a wider spread in the ordination, encompassing the entire range of the NMDS1 axis and overlapping substantially with males in areas associated with intakes of flounder, mud snails and crabs. Ellipses were calculated for the 32 birds with three or more observations, and the distribution of ellipse sizes (Appendix 3) suggested there were nine birds with very small ellipses that could be considered specialists (Figure 6, upper). These birds ate only one or two prey types each across an average of six videos each. Eight males ate almost exclusively *Potamopyrgus* while one female ate only worms. When tested using another hglm model, there appeared to be no major difference in the intake rates of specialists when compared to generalist birds.

Table 1: Zero-one inflated beta model results, including three sections for each. The first (bill) models proportions that are neither 0 or 1. Zoi models the probability that a proportion is either 0 or 1, and coi models the probability that a proportion, if either 0 or 1, is 1 rather than 0. This can be used to indicate the probability that individual birds may specialise on the prey item. Estimates are considered significant if their 95% C.I. does not include zero.

	<i>Estimate</i>	<i>95% C.I.</i>
Potamopyrgus model		
<i>Intercept:</i>	-0.52	-3.04, 2.45
<i>zoi Intercept:</i>	5.72	1.95, 10.23
<i>coi Intercept:</i>	32.44	14.83, 66.01
<i>bill</i>	-0.01	-0.04, 0.01
<i>zoi_bill</i>	-0.05	-0.10, -0.02
<i>coi_bill</i>	-0.33	-0.66, -0.15
Worm model		
<i>Intercept</i>	-5.72	-10.02, -1.57
<i>zoi intercept</i>	12.01	6.61, 18.85
<i>coi intercept</i>	-18.62	-33.16, -9.25
<i>bill</i>	0.05	0.01, 0.09
<i>zoi_bill</i>	-0.01	-0.17, -0.05
<i>coi_bill</i>	0.15	0.07, 0.28

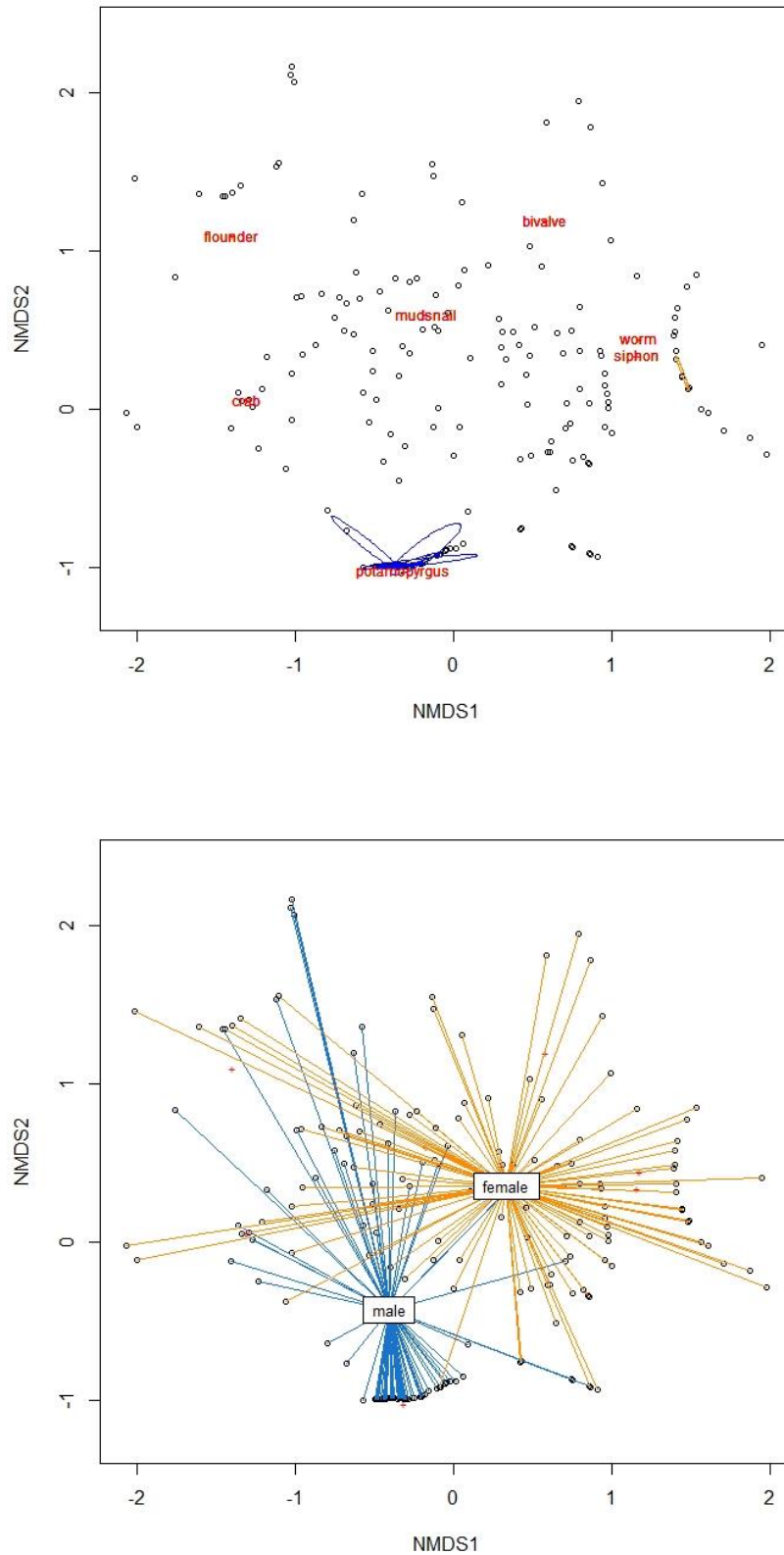


Figure 6: NMDS ordination plots of intake rates. The upper plot shows the relative spacing of each prey type relative to observations with ellipses showing the dietary range of nine specialist birds that ate only one or two prey types (males in blue, females in gold, ellipse areas <0.1 units). The lower plot shows the distribution of observations of intake rates for both sexes.

Factors affecting intakes of the different prey types

Hurdle lognormal models tested the effect of a variable on both the intake rate of a particular prey item, and the likelihood that a prey item was taken or not (this is the hurdle component). Only for two prey types, *Potamopyrgus* and *Cyclomactra* bivalves, did any variables have an influence on intake rates. For *Potamopyrgus*, bill length had a very slightly negative effect on intake rates as longer-billed birds (females) generally took fewer prey per unit time (Estimate: -0.02, 95% C.I.: -0.03, -0.01). Additionally, the proportion of time spent sewing had a huge positive effect on intake rates, dwarfing the effect of bill by several orders of magnitude (Estimate: 2.82, 95% C.I.: 2.35, 3.29). For *Cyclomactra*, males took fewer bivalves than females (Estimate: -1.29, 95% C.I.: -2.51, -0.04).

The hurdle component of the models showed that across all prey type intake models one trend becomes apparent — a bird's dominant foraging mode greatly influences whether a prey type is taken at all (Table 2 – full model outputs provided in Appendix 5). Birds that were sewing were much more likely to take *Potamopyrgus* and much less likely to take *Cyclomactra*, crabs, flounders and *Amphibola* mud snails. Birds feeding visually were more likely to take worms. Other significant influences on the likelihood of prey type consumption were detected (bill length positively for worms and negatively for crabs, depth positively for *Cyclomactra* and siphons and negatively for flounders, pacing rate positively on siphons; see Table 2) but their magnitudes were small in comparison to the effects of foraging mode.

Table 2: Hurdle estimates of significant variables influencing whether prey items were taken or not. Rows are prey types, columns are characteristics of the bird and its foraging behaviour, as well as an intercept for comparison. Positive values indicate greater likelihood of a 0 intake with an increase in the variable, whereas negative means the prey item was more likely to be eaten. Mean estimates are displayed, followed by a 95% confidence interval of these means. Final models did not include all the same variables; bill or depth were included as alternatives, as were proportions of time spent in each foraging modes.

Prey Type ¹	Intercept	Bill	Ave. Depth	Pace rate	Sewing	Visual
<i>Potamopyrgus</i>	-6.02 (-11.60, -1.38)	-- ²	N/A ³	--	-3.46 (-7.53, -0.61)	N/A
Worms	12.17 (5.94, 20.16)	-0.10 (-0.17, -0.04)	N/A	--	N/A	-4.65 (-7.19, -2.50)
<i>Cyclomactra</i> sp.	1.28 (-0.87, 3.45)	N/A	-0.02 (-0.04, -0.01)	--	8.20 (2.41, 20.11)	N/A
Siphons (from <i>Cyclomactra</i>)	11.02 (5.91, 18.16)	N/A	-0.06 (-0.12, -0.02)	-1.22 (-2.49, -0.13)	--	N/A
Crabs	-5.61 (-10.93, -0.90)	0.05 (0.01, 0.11)	N/A	--	3.99 (1.70, 6.87)	N/A
Flounders	-2.20 (-4.99, 0.46)	N/A	0.03 (0.02, 0.05)	--	10.38 (4.18, 20.74)	N/A
<i>Amphibola</i> sp.	2.27 (-3.52, 9.67)	--	N/A	--	3.79 (1.03, 7.31)	N/A

¹ n = 4665 for *Potamopyrgus*, 397 for worms, 82 for *Cyclomactra*, 21 for siphons, 51 for crabs, 95 for flounders, and 154 for *Amphibola*.

² "--" denotes a variable that is included, but non-significant in the model.

³ "N/A" denotes a variable that is not included in the selected best model represented in the above table.

Models that were run with sex instead of bill or average depth gave similar results. Sex influenced intake rates only for *Cyclomactra*, where males were less likely to consume these bivalves than females (Estimate: -1.29, 95% C.I.: -2.51, -0.04). Surprisingly, despite many males specialising on *Potamopyrgus*, there was no statistically significant relationship between sex and intake of this prey type.

The final GLM analyses indicate that there may be an influence of individual preference on the intake of each prey type, particularly for three of the observed prey items: *Amphibola*, flounder and worms. All models returned a ratio of residual deviance to residual df greater than 1, indicating overdispersion, but for these three prey types the ratio was greater than 2 (Table 3). Additionally, there is moderate evidence for an influence of individuality on the foraging of both siphons and *Potamopyrgus* as these had a ratio of 1.7985 and 1.6722.

Table 3: Residual deviance and degrees of freedom per GLM model testing the likelihood of a prey item being taken. The greater the ratio of deviance to d.f., the greater the overdispersion implying the presence of individual preference on choice of prey type. Of particular note is the high ratio for flounder, *Amphibola* and worms, implying a strong presence of individuality on the likelihood that a bird will eat these prey items.

Prey Type	Residual Deviance	Residual d.f.	Deviance: d.f.
<i>Potamopyrgus</i>	53.510	32	1.6722
Worms	69.374	32	2.167924
<i>Cyclomactra</i>	36.192	31	1.16748
Siphons	32.373	18	1.798502
Crabs	39.752	31	1.282329
Flounder	89.074	33	2.699208
<i>Amphibola</i>	74.681	32	2.333775

Discussion

This study demonstrates that foraging patterns in Bar-tailed Godwits differ noticeably between individuals, based both on sex and corresponding bill lengths. Bar-tailed Godwits are known to be relatively generalist feeders taking a range of mudflat dwelling prey (Smith & Evans 1973; McCaffery & Gill Jr. 2001), confirmed here by the diversity of prey items observed to be taken across all observations. The depths at which prey were taken also were found to vary significantly, which suggests the possibility of variation in dietary composition between individuals of different bill lengths. Prey types such as crabs, flounder, mud snails and *Potamopyrgus* were all retrieved at relatively shallow depths in the mud compared to the deeper bivalves, worms and siphons. While these

measurements are based off estimates of probe depths of prey captured, they act as a proxy for the depths of available prey items in lieu of vertical distribution sampling of prey items in the mud, showing that the deeper buried prey types were largely out of reach of male birds (Figure 2). At best, prey types such as worms and bivalves were within reach for males probing the full length of their bill, however Figure 3 shows that shorter billed birds generally did not try to probe this deep, further suggesting differences in intake rate related to bill length.

In addition to these descriptive patterns, the three foraging modes identified were distinguishable by more than simply the differing pacing rates shown in Figure 1. Godwits and other shorebirds were already known to use both tactile and visual foraging methods (Young 1989; Lourenco *et al.* 2016), however I also identified dabbling behaviour which would use a combination of both tactile and visual techniques. A bird engaging in sewing would repeatedly probe at the mud's surface and consume anything it encountered, thus exhibiting tactile foraging and is likely the behaviour described as 'tapping' observed heavily in males by Pierre (1994). A bird foraging visually acted as the name suggests, probing occasionally where it saw potential prey items. For this reason a visually foraging bird had a higher search speed as it needed to cover more area to ensure it found enough food (Dias *et al.* 2009). Dabbling birds showed a mixture of both visual and tactile foraging actions, keeping their bill tip to the mud and stirring up sediment while walking, noticing anything they disturbed such as flounder.

Influences of sex and size on foraging patterns

The first analyses of intake rates showed that shorter-billed birds had slightly higher intakes overall than their longer-billed counterparts, a trend that was matched in comparisons of the sexes (males higher than females). This finding is supported by Pierre (1994), who also found that males were more successful (in terms of higher numerical intakes) than females. In addition to this, I found that variability also increased with bill lengths, with some females being extremely successful in a foraging bout while others fared poorly. Variability in the diets seems to stem largely from prey types observed to be eaten in each foraging bout. I found that in foraging bouts with higher intakes (over 0.1 g AFDM per minute), the females with the highest intakes had high proportions of either crabs or *Amphibola*. Males with the highest intake rates observed in foraging bouts all ate high proportions of crabs, except for one that consumed a high proportion of flounder. Of the eighteen highest intake rates observed across both sexes, twelve consumed a large proportion of crabs. Intake of crabs largely appeared to be opportunistic and not influenced by individuality. Despite this, these intake rates clearly had a major effect on total biomass intake rate, suggesting that they were a valuable prey item when

captured. The high intake rates due to a high proportion of *Amphibola* show the value in being an individual with a preference for these snails. In addition to the variability in diet composition between individuals, foraging modes also show a very clear pattern where males heavily favoured sewing, whereas females were more variable in their foraging mode usage.

There were also differences in the prey types taken by birds of different bill lengths, and this is partially supported both by the proportional analysis and the log-normal hurdle model results. The clearest difference highlights the disparity in bill lengths – shorter billed birds (males), primarily ate *Potamopyrgus* whereas longer-billed birds (females) were more likely to take larger, deeper prey items such as worms. Furthermore, specialists on either of these prey types were apparent; more than half of the males in the sample (8 of the 15 birds) specialised almost entirely on *Potamopyrgus*, and one female (AMT) specialised entirely on worms. The general trend with all prey types was that the biggest influencing factor on intake rates of prey types was the chosen foraging mode used by the bird. In all prey types except siphons, foraging mode plays a massive role in influencing whether a prey type is taken or not. Effects of bill or average depth are present in five of the seven prey types but these effects are negligible in comparison to the effect that foraging mode has on item intake. Foraging by sewing, for example, greatly reduces the chance that a bird will fail to consume any *Potamopyrgus*, however sewing appears to decrease a bird's chances at obtaining any other prey item. In the context of *Potamopyrgus*, this makes sense given their abundance across the mudflats – they were perhaps the most readily available prey source. An explanation for the wide range of depths at which they were obtained that is shown in Figure 2 is simply that sewing birds repeatedly probed and overshot their prey items, given that their foraging was largely tactile. Regarding all other prey types, the marked difference between sewing behaviour and the other two foraging methods is the major reason models that include sewing have the most evidence to support them based on Bayes factors, which are an index used to compare models and select that with the most evidence supporting it (Jarosz & Wiley 2014). For example, birds that consumed crabs did not engage in any sewing behaviour at all except for in two videos, and a similar pattern was observed in bivalves. The disparity wherein sewing birds did very little of the other foraging modes further highlights the significance of sewing in these models.

Interestingly, these models demonstrate that very few factors influence the actual intake rates of prey items when they are taken. No general pattern was observed for any prey types except *Potamopyrgus* and *Cyclomactra*. Both bill length and proportion of time spent sewing showed an influence on the intake rates of *Potamopyrgus*, likely because sewing behaviour allowed birds to eat large quantities as *Potamopyrgus* were abundant across the entire mudflat area and birds did not move particularly fast when eating them. The effect of bill length on intake rate was very small by comparison and likely

appeared in the model due to the much higher proportion of time spent foraging by sewing by shorter-billed birds (males, shown in Figure 4). Sex was the only factor providing any influence on the intake of *Cyclomactra* as they would have been buried in the sediment at a depth that males with shorter bills could not reach, but no general trend in intake rates with respect to bill length was observed. The lack of any major influences in the intake rates from variables such as bill or sex suggests that intake rates of most prey items were simply opportunistic or due to individual preference.

Siphons in particular were taken only rarely – just 21 times across all 215 videos, clearly showing that they were not a major targeted prey item for most birds. Siphons are part of the foraging morphology of a bivalve buried in the sediment, poking up to the surface through which the bivalve pumps water to filter out food items. The benefit of having a longer siphon is that the bivalve itself can bury itself deeper and thus have a better chance at avoiding predators (Zwarts & Wanink 1989). These siphons are muscular and can retract back into the shell (Trueman 1966) as a defence mechanism in response to predators (Smee & Weissburg 2006). These were the only prey item for which pacing rate/searching speed had any influence on their intake, showing that faster-pacing birds were more likely to consume siphons. This trend makes sense, as the siphons were extended from a buried bivalve that would withdraw them into its shell if disturbed. Thus, to successfully take any siphons at all, birds had to be fast to capture a siphon before it was withdrawn. However, this is likely not the major prey item the godwits targeted but was simply all they could manage to get when trying for bivalves. Given that the siphons leave visible holes in the mud's surface, they would have indicated the location of a potential prey item and so substantially more complete or partial bivalves were consumed than simply the siphons themselves.

Niche separation

My evidence suggests that there may be some niche separation or resource partitioning between the sexes based on their foraging equipment morphology, a pattern that can avoid intraspecific competition (Nebel & Thompson 2011). While I have demonstrated that many prey items have no discernible difference in intakes based on sex or morphology, the presence of differences in intake rates of certain prey types (worms and *Potamopyrgus*) between sexes show there is indeed variation between diets. This is particularly evident in the ordination plots (Figure 6, lower panel) where it shows that while there is significant overlap in diets between males and females, males have substantially narrower diets. This is even more pronounced in the intake rate data shown in Appendix 4, that indicate that females were the only birds to eat siphons and almost all bivalves, in addition to the sex biases in worm and *Potamopyrgus* intakes. Additionally there is a noticeable absence of *Amphibola* in

the diets of smaller males, possibly due to limitations on gape width of the smaller birds (Zwarts & Blomert 1992) that prevents them from physically fitting prey in their mouths. This could suggest a gradual separation of niches within a sex as well. While these patterns appear visible in the data, relationships were not significant in the models for many prey items, possibly due to the high variation between individuals, which will be discussed next.

It is worth noting that any niche separation in dietary composition does not appear to result in large-scale spatial segregation as seen in other studies (Duijns *et al.* 2014) as both males and females are present in relatively equal numbers on the same mudflats. However, there is a latitudinal trend in bill lengths of birds breeding in Alaska (Conklin *et al.* 2011) where the more northern birds tend to be smaller than their southern counterparts. There is no obvious pattern of size variation around New Zealand (Conklin *et al.* 2011), suggesting that any differences in foraging based on bill lengths on the non-breeding grounds are the by-product of selection pressures acting on the breeding grounds. A similar proposal has been made about Curlew Sandpipers (*Calidris ferruginea*) by Puttick (1981) where sexual dimorphism was likely due to competition on the breeding ground rather than due to prey availability limitations on their non-breeding grounds. The apparent lack of any such spatial segregation in these godwits suggests that all niche variation between individuals simply occurs in diet choice.

Evidence for specialisation and individual preferences

I found evidence for both specialisation and individuality in the study population of godwits. Oudman *et al.* (2016) proposed that individual preferences may be pre-existing and lead to changes in behaviour and morphology rather than morphology driving foraging behaviour (though in the context of gizzard size and patch residence time). In my study, eight of 15 males ate exclusively or almost exclusively *Potamopyrgus*, a pattern unexplained by bill as the specialists occurred across the entire sample range of male bill lengths. One female of average bill length consistently ate only worms, an observation explained by no variables in the data. Clearly, males were more likely to be specialists but the cause of this is uncertain. This could be due in part to the narrower diet range observed in males as shown in the ordination plots, and certainly it is harder for males to access buried prey such as worms and shellfish, but neither of these factors would limit males to feeding on *Potamopyrgus*. Furthermore, other prey items such as *Amphibola* and flounders may not be taken randomly across the population, as only certain birds (that were not grouped by morphology) appeared to have a penchant for taking these prey items (e.g. intake rates in Appendix 4). These birds are not specialists, but nevertheless have diet preferences (or proficiencies) that highlight the individuality evident in the

population. The GLM models that tested the presence of individuality examined the data by bird rather than by video and could not include other environmental variables that varied across videos. As these environmental factors did not show any large influence in the earlier log-normal models they could be excluded but may be a contributing factor for some of the overdispersion, but not enough to overrule the influence of individuality on diet choice. Additionally, these models did not include foraging mode data as these also varied between videos and were shown to be heavily prey-specific. Because of this, the chosen foraging mode is indicative of the prey the bird is choosing to hunt which thus results in patterns of individuality, of which some are clearly evident in the intake data (Appendix 4). Instead, these models examined the effects of the bird's morphology and individual preference on likelihood of intake of a prey type in a foraging bout regardless of the chosen foraging mode of a bird. It was surprising that the intake of worms was influenced by individuality given that so many longer-billed birds foraged on them, but this influence could be because many birds that took any worms only took them in a minority of foraging bouts, compared to several others who took them frequently. The moderate result of individuality influencing the intake of *Potamopyrgus* highlights the fact that while most birds took this prey at some point, there was variation between individuals in how often they took them during foraging bouts, as some birds took *Potamopyrgus* in every bout they were observed. This includes the true specialists foraging only on *Potamopyrgus*, and shows how individual preference can play a role in diet choice of individual godwits.

There is little explanation for causes of the apparent individuality seen in birds or what drives them to forage the way that they do. Their intake rates were no higher than those of generalists. It is possible that these differences are ontogenetic, and result from subtle differences in experience or proficiency developed during birds' formative years. Juvenile birds are known to be substantially less proficient at foraging than adults (Weathers & Sullivan 1989; Hand *et al.* 2010). As juvenile birds grow, they gradually develop better foraging skills, but how this occurs in godwits is unknown. Juvenile godwits are known to wander widely in New Zealand before settling at non-breeding locations (Battley *et al.* 2011), so it is possible that these explorations influence how a bird learns to forage as an adult, e.g. some birds might never encounter flounder and so don't learn how to capture them. Prey items that a bird learns during this developmental period could explain also why some birds simply don't feed on obviously visible prey items such as mud snails – these may not be prey items the bird knows how to process and so simply ignores them when hunting for more familiar prey items. Such experiences as the birds age and develop their foraging proficiency could culminate in the individual foraging patterns observed and could account for both specialists and generalists that are flexible with their foraging behaviours. Studies of handling time are important to produce a cost/benefit analysis for a bird consuming each prey item and could provide further evidence that some birds are better at foraging

on specific prey types than others. Handling time is a metric most often used to determine the profitability of prey items, so that larger items with more biomass may not be as profitable if they require extensive handling (van de Kam *et al.* 2004). Individual proficiency at foraging on specific prey items could be examined but would need to be conducted in a captive setting as it would be impossible to study wild birds' proficiency of foraging on prey items that they simply do not eat when given the choice.

Future studies

Several factors could be considered when planning future studies to further understand heterogeneity in godwit foraging. The first of these would be to expand sampling area as birds frequently foraged on other areas of the mudflat, both upstream and on the south side of the river, any variation in which could not be accounted for in this study. Additionally, female godwits in particular forage in belly deep water, conditions in which crabs and other invertebrates would be more active (Luppi *et al.* 2013). Given that water obscures these prey intakes, identification was impossible so potentially a major intake period for crabs was missed in the analyses and assumptions of prey type and size had to be made. Videos taken later in the season could eliminate any effect of time since a bird's arrival from migration, as all videos here were taken within each bird's first two weeks since arriving on their non-breeding grounds. Any effects of time since arrival were tested to assess whether they played a major role in the data and are discussed further in Chapter 3. Additionally, Durell (2000) argues that social status may also further influence the prey selection of individuals, as more dominant individuals may have access to the more profitable prey items in the same habitat. Determining the dominance hierarchies within a population of godwits is an avenue worth exploring in a future study.

Overall, however, the models show that the greatest influence on intake rates and diet choice stems from the chosen foraging mode of an individual bird. Not all birds forage in the same fashion, and so are accessing different prey types via their preferred foraging method. Prey-specific foraging tactics are not an unusual concept, as different prey types behave differently and so particular strategies are required to hunt them based on these behaviours (Bowen *et al.* 2002). The prey types tend to behave differently, so it follows that different modes would be chosen, and this is where the biggest patterns relative to bill length are found. Prior to capturing prey, it appears that godwits make decisions to forage in particular ways based on what they can access and because of this, the foraging mode cannot be excluded from the models. By focusing largely on one extremely common prey item, shorter-billed birds manage to maintain a consistently higher intake rate. Longer-billed birds more often have a varied diet, but overall intakes are far more variable, taking prey items in much lower quantities than

their shorter-billed counterparts. Further studies of spatial patterns and density of prey items would confirm that these other prey types such as worms are far less common and thus the faster searching modes of foraging would be ideal for covering more ground, however the high variability of these longer-billed birds suggests that much of the intake is opportunistic, taking whatever prey types they can find while they search. A further cost-benefit analysis could highlight why the shorter-billed birds have higher intake rates, potentially to compensate for the inability to access all prey types as the longer billed bird can and would highlight the complexity of godwit foraging decisions.

Chapter 3:

Carry-over effects of trans-Pacific migration on intake rates of Bar-tailed Godwits are small

Abstract

Birds that routinely undertake long-distance migratory flights are known to drastically change their body composition and physiological processes during flight. Fat is the primary source of energy sustaining these flights; however, protein is also heavily catabolised from both muscle and internal organs. Birds arriving after extreme long-distance flights (such as the >11,000 km trans-Pacific flight of southbound Bar-tailed Godwits *Limosa lapponica baueri*) are expected to arrive on the non-breeding grounds with substantially reduced gastro-intestinal (GI) tracts. Given links between the size of the GI tract and its processing ability, newly arrived birds potentially face impaired food processing ability. Here I test for carry-over effects of migration on both diet and energy intake in newly arrived godwits in New Zealand. I used videography to repeatedly record individual godwits foraging over approximately two weeks after their arrival back at their non-breeding site. I estimated intake rates based on video observations and examined the effect of time since arrival on both overall intake rates and diet composition of birds. I found evidence for a slight increase in intake rates over time and an increase in the intake of the hard-shelled mud snail *Amphibola crenata*. This increase in consumption of mud snails likely reflects an increase in gizzard mass and strength with time since arrival. Overall, however, any changes with time were small, and there was no indication that the 8–10-day duration of their migratory flight results in substantial impairment of foraging ability. This may be because godwits at the study-site had a broad diet that also included small or soft items that would be easily processed even with a reduced GI tract. Bar-tailed Godwits, despite making the longest non-feeding flight documented among birds, are able to compensate adequately during their recovery period.

Introduction

The long-distance flights of migratory birds are enabled by a host of morphological and physiological adjustments that result in deposition of extensive fat and protein reserves prior to migration along with enhanced foraging and metabolic capacities (Odum 1960; Jehl Jr. 1997b; Lindström *et al.* 1999; Battley *et al.* 2001; Guillemette *et al.* 2012; Bairlein *et al.* 2015). While fat provides the vast majority of the energy in multi-day endurance flights (McWilliams *et al.* 2004), protein breakdown can also be extensive (Battley *et al.* 2000; Bauchinger & McWilliams 2012). This could result in reduced physical capacities upon arrival as birds often arrive severely emaciated, at times half the mass they were upon departure (Piersma 1998).

The gastro-intestinal (GI) tract is known to be particularly labile. Across species, the liver and intestine are disproportionately reduced during flight (Bauchinger & McWilliams 2012), and in some species the gizzard has been documented to be reduced before or during departure on migratory flight (Jehl Jr. 1997a; Biebach 1998; Piersma & Gill 1998; Battley *et al.* 2000; Landys-Ciannelli *et al.* 2003). Intake

rates can be directly limited by the size of the GI tract (van Gils *et al.* 2005a; van Gils *et al.* 2005b), so prolonged migration may have carry-over effects on subsequent foraging behaviour and energy intake. Digestive tract mass is both hugely flexible and reversible (Starck 1999; Starck & Rahmaan 2003), and given the rate at which substantial enlargement of the gizzard is possible, with increases of almost 150% occurring in only 6 days (Dekinga *et al.* 2001; van Gils *et al.* 2003), recovery ought to be discernible over quite short time-frames. Indeed, experimental work on passerine migrants suggests that assimilation efficiency is also affected by migration, increasing over a matter of days when at stopover sites (Karasov & Pinshow 2000; Gannes 2002).

The longest documented flight of any land bird is the post-breeding flight of the Bar-tailed Godwit (*Limosa lapponica baueri*), migrating across the Pacific Ocean from Alaska to New Zealand (McCaffery & Gill Jr. 2001; Battley & Piersma 2005b). This 11–12,000 km flight can take 8–10 days to complete (Battley *et al.* 2012), making godwits an ideal candidate in which to test for a migration-related effect of arrival body condition on foraging performance. Here, I studied both the changes in overall intake rate of birds newly arriving from migration, and the composition and relative changes of their diet as they recovered from migration and potentially regained full gut functionality. Prey choice could change during recovery if newly arriving birds initially are unable to physically process hard prey items due to having reduced gizzard sizes (van Gils *et al.* 2003). I therefore predicted that intake rates and the consumption of hard prey would increase with time since arrival from migration, if gut capacity limits intake in this species.

Methods

Data Collection and Processing

Data were collected for this chapter by the methods described in Chapters 1 and 2. In brief, birds were digiscoped at the Manawatū River Estuary, New Zealand (40°28'30" S, 175°14'30" E), from 4 September to 24 October 2017. Immediately prior to and following the videoing period, intertidal benthos were collected from 40 sites and ash-free dry mass (AFDM) determined for the main prey items. These data were used to predict biomass values for prey items observed being consumed by godwits (polychaete worms, *Potamopyrgus* and *Amphibola* mud snails, crabs of multiple species, juvenile flounder (*Rhombosolea* sp.), bivalves (*Cyclomactra*), and the siphons off these bivalves eaten separately).

Video selection

Over 900 videos of 54 individually-marked birds were recorded, from which I selected 215 videos of 34 birds for analysis. These were selected on the basis of (1) complete representation of the range of bill lengths in the population, (2) birds for which videos were available from soon after arrival on the non-breeding grounds (determined from daily flock checks), and (3) preferably for which multiple videos were available for the two weeks after arrival. Where more than one video was available on a given day, the one with best image quality was selected. The final selection had a mean of six videos per individual (range 2–11), with 24 birds being videoed on their first day back in New Zealand (Appendix 1). The videos were analysed using the software BORIS as explained in Chapter 2.

Data analysis

Statistical analyses were performed in R version 3.5.1. Initially, linear regressions were run and plotted for each individual bird to gauge any significant trends in total intake rates, then hierarchical generalized linear models (HGLMs) were used to analyse the effect of time since arrival on overall intake rates of the birds, using the R package *hglm* (Ronnegard *et al.* 2010). A dispersion model included in the overall model allowed the effect of each variable on the intake rate variance to be calculated as well. Variables were log-transformed before analysis, and in addition time since arrival (where day 0 equals the day of arrival at the site) and other variables known to affect intake rates (Chapter 2) were included in HGLMs with a Gaussian distribution.

In addition to testing for changes in overall intake rate, I also tested for changes over time in the intakes of different prey types. As birds usually took only a few prey types during an observation period, the data included high numbers of 0 intake values. Initially, all three documented modes of foraging (visual, tactile, dabbling) were tested for changes over time, given that these are known to have the greatest influence on prey choice of foraging godwits (Chapter 2), using hurdle log-normal models of the proportions of time spent in each mode. These foraging modes are examples of prey-specific foraging behaviour in which each is suited to hunting certain prey types. Following this, other factors known to have significant effect on intake rates as found in Chapter 2 were included in the models.

The zero-inflated intake rate data for each prey type were analysed using hurdle log-normal models from the R packages *rstan* and *brms* (Bürkner 2017; Stan Development Team 2018). These models can analyse zero-inflated data and can also model presence or absence of a prey type in the diet of an individual (Dicken & Booth 2013). They contained two parts, the first of which provides estimates on trends in the overall intake rates. The second part provides hurdle estimates that indicate the

likelihood of the intake rates of the prey items being zero. Significance of estimates for variables in the model was evaluated by whether the 95% confidence interval of the mean estimate excludes zero (in which case the relationship is considered significant). The flexibility provided by these these log-normal hurdle models allowed me to determine the variables that affect whether a prey item was taken or not, and how large an effect this was on the quantity of each prey item taken.

Results

Time since arrival was not found to have any significant effect on any proportion of time spent using a foraging mode except for the hurdle model of dabbling, where dabbling was indicated to be slightly less likely to occur with time since arrival (Estimate: 0.10, 95% C.I. 0.01–0.19). Linear regressions of individual birds' total intake rates over time suggested that for the majority of birds any change in intake rates was very slight except for a couple of birds (Figure 1). More detailed HGLM analyses across all birds suggested that time since arrival had a small but discernible impact on total intake rates (Table 1). Furthermore, intake rates also became slightly less variable with time since arrival (Table 1). Analyses of the individual prey items indicated that time since arrival affected only two prey types, flounder and *Amphibola* (Table 2). The likelihood of flounder being taken at all decreased with time (Hurdle Estimate: 0.19, 95% C.I. = 0.07–0.34, meaning the chance of a bird taking no flounder at all increased over time). Time since arrival affected both the intake rate and hurdle likelihood *Amphibola* mud snails being taken. Intakes of *Amphibola* increased with time (Estimate: 0.08, 95% C.I. = 0.01–0.16) while the likelihood of consuming no *Amphibola* at all decreased (Hurdle Estimate: -0.16, 95% C.I. = -0.27 to -0.06).

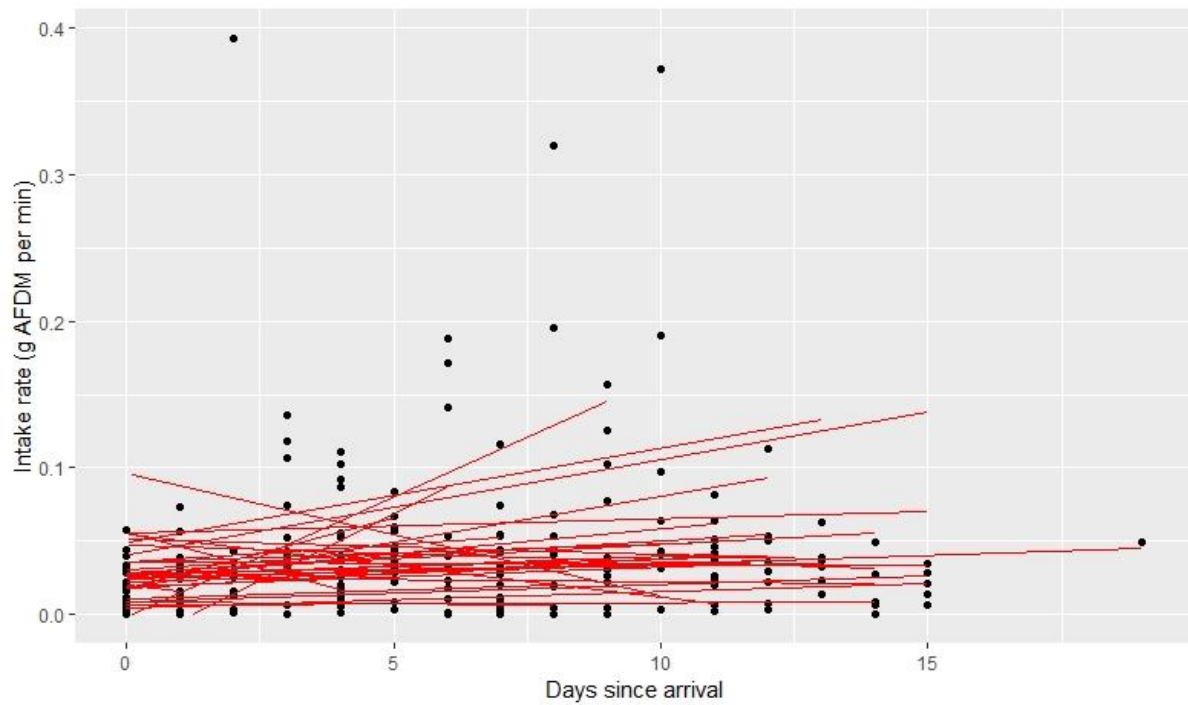


Figure 1: Linear regressions of total intake rate per individual bird, showing that most birds showed either no, or only a very slight, increase in intake rates over time since they arrived from migration.

Table 1: Estimates and variances from HGLM analyses of the effect of time since arrival from migration on the total intake rates of godwits.

<i>INTAKE RATE</i>	<i>Estimate</i>	<i>Standard Error</i>	<i>p-value</i>
<i>Intercept</i>	-2.2226	0.5563	<0.0001
<i>Time since arrival</i>	0.0516	0.0142	0.0004
<i>VARIANCE:</i>			
<i>Intercept</i>	-3.5384	0.7339	
<i>Time since arrival</i>	-0.0853	0.0243	

Table 2: Effects of time since arrival on intake rates of specific prey items. Where no significant effect is observed (95% CI includes 0), this is denoted by '--'. If the variable was not included in the model due to not being significant to the intake rate as found in Chapter 2, this is denoted by 'N/A'. Where an effect is apparent, this is written as an estimate in relation to the intercept listed above, then the 95% CI in parentheses. This estimate is relative to the intercepts in the upper two rows. Hurdle values indicate the likelihood of an intake rate to be 0 in relation to time since arrival. Full model outputs included in Appendix 5.

	<i>Potamopygus</i>	Polychaete	<i>Cyclomactra</i>	Crabs	Flounder	Siphons	<i>Amphibola</i>
Intercept	-5.10 (-6.32, -3.83)	-7.61 (-11.43, -3.83)	-4.81 (-6.38, -3.23)	-2.36 (-6.62, 1.73)	-5.01 (-5.93, -4.10)	-6.97 (-9.42, -4.31)	-4.40 (-5.08, -3.73)
Hurdle (hu)	-4.96 (-9.96, -0.73)	11.00 (5.71, 18.04)	2.71 (1.43, 4.18)	-4.59 (-9.82, -0.09)	-2.27 (-3.85, -0.83)	10.76 (6.74, 16.27)	2.46 (1.45, 3.71)
Intercept							
Time	--	--	--	--	--	--	0.08 (0.01, 0.16)
Bill	-0.02 (-0.03, -0.01)	--	N/A	--	N/A	N/A	N/A
Depth	N/A	N/A	--	N/A	--	--	N/A
Sewing	2.95 (2.56, 3.33)	N/A	--	--	--	N/A	--
Visual	N/A	--	N/A	N/A	N/A	N/A	N/A
Time (hu)	--	--	--	--	0.19 (0.07, 0.34)	--	-0.16 (-0.27, -0.06)
Bill (hu)	0.04 (0.01, 0.09)	-0.08 (-0.14, -0.03)	N/A	0.07 (0.02, 0.12)	N/A	N/A	N/A
Depth (hu)	N/A	N/A	-0.02 (-0.03, -0.01)	N/A	0.04 (0.02, 0.06)	-0.05 (-0.10, -0.01)	N/A
Pace Rate (hu)	N/A	N/A	N/A	N/A	N/A	-1.24 (-2.26, -0.31)	N/A
Sewing (hu)	-3.88 (-7.50, -1.34)	N/A	7.16 (1.83, 17.97)	3.57 (1.49, 6.42)	10.09 (4.37, 21.73)	N/A	3.61 (1.23, 6.87)
Visual (hu)	N/A	-3.63 (-5.14, -2.28)	N/A	N/A	N/A	N/A	N/A

Discussion

Godwits arriving after an 8–10-day non-stop flight would be expected to have a severely reduced digestive system, but I found little evidence that their gross intake rates changed over the weeks following their arrival in New Zealand from Alaska. There was a slight increase in biomass intake rates with time, though for most birds any change was negligible. There was, however, evidence for an increase with time since arrival in both the intake rate of the mud snail *Amphibola* and the likelihood of it being taken. *Amphibola* is a medium–large surface-dwelling gastropod that is always visible and detectable on the tidal flats. Because of its hard shell, *Amphibola* would require greater force to crush and process compared to other prey types on the mudflat, a task performed by the gizzard. Reduced

gizzard mass such as that observed in newly arrived birds would likely result in reduced processing capacity (van Gils *et al.* 2003; van Gils *et al.* 2005a) until the bird recovers from migration. Intake of *Cyclomactra* was expected to exhibit an increase over time given that they also have a hard shell, however this did not occur. This was likely because bivalves were often consumed as fragments in this study; either the siphon was extracted or the godwits managed to consume flesh without the shell, altogether negating the cost of processing shell material.

It was important to test for changes of foraging mode over time given that in Chapter 2 I found that foraging mode has the greatest effect on intakes rates of prey items. These tests showed no effects of time on any mode except for a slightly decreased likelihood of dabbling. Dabbling behaviour increased the likelihood that flounder would be consumed (Chapter 2), so this decline in dabbling likelihood could explain the decline in likelihood of flounder captures. Seasonality is another potential cause of temporal changes in godwit intake of flounder, given the seasonal timing of flounder spawning (Wuenschel *et al.* 2009; Amorim *et al.* 2016), however a study of New Zealand Fairy Terns (*Sternula nereis davisae*) found that flounder were regularly recorded at sampling sites right through to January (Ismar *et al.* 2014). The decreased likelihood of flounder captures over time could instead be due to increased profitability of less mobile prey such as *Amphibola* as the birds' gizzards recover, but population depletion over time could also be a cause of the decline in likelihood of flounder capture (Zwarts & Wanink 1984). In a future study, it would be beneficial to carry out density analyses of prey such as flounder throughout the sampling period as this could provide information on the relative availability of flounder, something that was not examined in this study.

Geolocator data from the study population confirm that most birds return directly to their 'wintering' site rather than stopping elsewhere first (Conklin *et al.* 2017, Battley, unpub. data). This means that these findings are accurate for newly arrived birds. While effects of migratory recovery were detected, these effects were very small in comparison to the other behavioural effects on diet, particularly that of the chosen foraging mode, where included in the model (Table 2). This could be because the array of prey available in this study likely allows newly arrived godwits to obtain enough energy from easily digestible prey types such as worms, flounders or the small *Potamopyrgus*. Similarly, van Gils *et al.* (2003) and Yang *et al.* (2013) found that Red Knots (*Calidris canutus*) arriving at stopover sites with small gizzards could adequately maintain intake rates due to the prevalence of small, soft or easily digestible prey items on the mud flats. It is less clear how strongly gizzard size affects individual choice and intake rates, as captive knots with small gizzards, when offered both high-quality and low-quality prey, still ate some less profitable prey (Mathot *et al.* 2017). This may explain why some *Amphibola* were eaten by some birds on the day they arrived back, even though the birds would have had reduced gizzard mass. To further augment our understanding of recovery from migration more studies

examining different aspects of recovery would help, including i), studies of energetics and handling time of prey items to determine optimal foraging patterns, ii) body mass measurements to determine the relationship between intake rates and individual mass gain to provide insight into the assimilation capacity of a recovering godwit and iii) measurements of daily activity levels to ascertain whether carry-over effects influence the relative amount of time spent resting compared to foraging as a bird recovers.

I have shown that any carry-over effects of endurance migration on the short-term intake rates of Bar-tailed Godwits at my study site are small. The only prey item for which an increase in intake rate was detected was the mud snail *Amphibola*, a result consistent with expectation based on reduced processing ability from an atrophied gizzard. This prey item was, however, taken in only a minority of observations (41 of 215) by a minority of individuals (16 of 34). Most of the diet of godwits consisted of prey that were small (e.g. the small snail *Potamopyrgus*) or soft (polychaete worms, bivalve parts, and flounder). It may be that the existence of a flight as prolonged and extreme as that of these godwits relies on there being a suite of easily-processed food that does not require much mechanical breakdown, so that carry-over effects are minimised.

Chapter 4:

General Discussion

Foraging modes and diet

Bar-tailed Godwits are variable in both their morphology and their foraging behaviour. Complex relationships influence both their general foraging patterns and how they recover from migration after flying the longest known migratory flight in the world. Their huge variation in bill length and body size between and within the sexes make them a prime candidate for studies of how variable morphology affects foraging strategies. Additionally, given the extreme distances over which these birds migrate, they are a species ideally suited for studies into the recovery processes that follow such an athletic feat. The presence of a well-studied, individually marked population at the Manawatu River Estuary further makes this species accessible for such a study. These mudflats are a valuable overwintering site for a small population of godwits and they were designated a RAMSAR site in 2005 (Manawātū Estuary Trust 2010), signifying the importance of the wetland habitat and therefore its value to studies like this.

The diet of Bar-tailed Godwits is known to vary seasonally. In their Alaskan breeding grounds they inhabit inland tundra environments and tend to forage at or above the surface on prey types such as beetles, flies and spiders, but they are also known to consume berries (McCaffery & Gill Jr. 2001). However, in their non-breeding grounds in New Zealand they inhabit largely coastal mudflat environments. Here they tend to forage on prey at or below the surface of the mud, requiring them to probe with their bills. Prey items found to be consumed by Manawatu birds include mud snails (*Potamopyrgus* and *Amphibola*), *Cyclomactra* bivalves and their siphons, polychaete worms, crabs and juvenile flounder (*Rhombosolea* sp.), further highlighting the diversity of godwit prey. Additionally, the birds used markedly different ways to obtain these prey items. The three major foraging modes (sewing, dabbling, visual) appear to be prey-specific, which is discussed later. While prey selection and overall intake rate varied across the population, this study found that for most prey types there was very little systematic difference in intake rates based on any factor included in the models. What was found, however, were patterns in the hurdle sections of the models. The models were not straightforward to interpret, but the hurdle component represents the significant jump between the heavily 0-biased intake rate data to those non-zero data and indicates the likelihood of whether an intake rate was zero or not (Ma *et al.* 2015). In all but one prey type model, the chosen foraging mode of a bird had a massive influence on whether a particular prey type was taken or not.

All three foraging modes were associated with their own distinctive searching speeds. Sewing foraging was the slowest whereas visual foraging birds moved fastest. A large contributing factor to this would be the prey items they were targeting and their relative density across the mudflats (Dias *et al.* 2009). Sewing was frequently used exclusively with very little foraging occurring via the other two modes. Shorter-billed birds (males) predominantly used this mode, and almost all sewing specialists were

males. Sewing behaviour was largely tactile, targeting prey items that were present in high densities so walking fast was not required to ensure birds ate enough items to sustain themselves. Sewing greatly increased both the chances of intake and the quantity of *Potamopyrgus* snails taken, which makes sense given the high frequency with which they occurred in benthos sampling. In places, *Potamopyrgus* reached such high densities that no other prey types were visible on the surface (pers. obs.). Visual foraging tended to target more sparsely distributed prey items that may also retreat into burrows in the mud if they detect a threat. Worms are a good example of this as worm-feeding godwits exhibited a significant relationship between likelihood of any intake and the proportion of time spent visually foraging. The more visual foraging a bird engaged in, the greater its likelihood of catching a worm. Polychaete worms can live in deep burrows in the mud, into which they retract to depths out of reach if threatened by a godwit or some other predator (Esselink & Zwarts 1989). By walking fast, godwits have a greater opportunity of both encountering and successfully capturing a worm as occasionally worms were visible on the surface but not for long when threatened. A similar pattern was highlighted by Withington (2015) who found that following capture of a worm, visual foraging Wrybills (*Anarhynchus frontalis*) had higher searching speeds likely because any other worms in the immediate area would have withdrawn due to disturbance.

Foraging modes such as dabbling or visual foraging were more interchangeable and both had faster searching speeds than sewing behaviour. Birds that did not exclusively sew engaged in visual foraging as an alternative, but did not engage in dabbling. Sewing behaviour was most often included in the models with the most evidence, but only positively influenced *Potamopyrgus* suggesting that it was a very prey-specific foraging mode. The prevalence of inclusion of sewing behaviour in the models with the most evidence does not rule out any effect of the other two foraging modes. Each mode was included in its own model but had to be run separately given that the metrics of each mode were proportions dependent on one another.

Prey types other than worms and *Potamopyrgus* exhibited notable relationships with each foraging mode, further supporting the links between foraging modes and specific prey. For example, bivalves were far less likely to be captured when a bird foraged by sewing. Here there was a significant relationship wherein dabbling birds were more likely to take bivalves in comparison to those visually foraging as well. This is perhaps surprising given that bivalves leave visible traces on the surface where their siphon protrudes, but dabbling foraging involves some tactile hunting suggesting perhaps the birds are using their sensitive bill tip to detect changes in pressure or movements in the mud from a bivalve closing its shell (Piersma *et al.* 1998; Nebel *et al.* 2005; Cunningham *et al.* 2013).

Crab activity is known to vary cyclically with tides (Backwell *et al.* 1998; Luppi *et al.* 2013). This perhaps explains why crabs displayed a similar relationship with foraging modes to that seen in bivalves. Dabbling birds were more likely to capture crabs than those using either of the other two foraging modes, and this could be because while dabbling they encountered crab burrows and could detect motion within them. Visual foraging was expected to have the greatest effect as crabs were visibly moving around on the mudflats while videoing was taking place (pers. obs.). However, these crabs could potentially be very vigilant and close to their burrows during low tide. Visual foraging alone may not have sufficed to capture them because of this. Both visual and dabbling foraging appeared somewhat interchangeable as dabbling also utilised a lot of visual hunting strategies. A possible explanation for this is that a bird would see where a crab was, then when it disappeared down a burrow the bird would dabble in the area to detect where the crab was hiding and then pull it up. Additionally, as dabbling most often occurred in patches of mud with a surface of water, what might have appeared to be dabbling might more likely have been the initial handling and manipulation of the crab. These are known to be difficult prey items for birds to manipulate and birds are known to be selective of size due to this, with large crabs requiring far more handling and dismemberment before they are able to be consumed as shown in studies of Curlews (*Numenius* sp.) (van de Kam *et al.* 2004).

Siphons were a complicated prey type for many reasons. They were the only one that was taken specifically as a portion of another prey type, and they were not eaten frequently, being taken only 21 times across all 215 videos analysed. Interestingly, there was no statistically significant relationship with any foraging mode. These siphons are the most readily available part of a bivalve as they protrude to or above the surface and are known to be eaten not just by godwits but by fish and many invertebrates as well through siphon cropping (Smee & Weissburg 2006; Nuñez *et al.* 2013). Because of this, they can be rapidly withdrawn from the surface as a defence mechanism (Trueman 1966), which would explain why the most significant relationship involving prey choice of siphons was the total pacing speed of the bird. Because siphons are a structural part of *Cyclomactra*, the density of this prey item is the same as that of the bivalves of which they are a part. It is worth noting, however, that during benthos sampling, there was a largely linear relationship between bivalve total size and the siphon length but this was not always the case, as some bivalves had shorter siphon lengths in proportion to shell size than others. In these cases, the siphons may have been attacked previously by a predator thus shortening the siphon. This would affect size estimate data as the siphon mass from a larger siphon that had been cropped by a predator would still provide more biomass than that of a smaller, uncropped bivalve siphon of the same length. Additionally, these siphons are known to regenerate in bivalves (Nuñez *et al.* 2013), and their length is known to influence the burying depth of an individual, thus affecting its chance of survival (Zwarts & Wanink 1989). This detail is relevant as

many of the bivalves sampled for biomass estimates were taken from depths below which godwits could reach, since the corer used in sampling went to 30 cm deep. These bivalves could likely have had greater biomass due to larger, intact siphons whereas those taken by godwits may have previously been cropped. This would reduce overall biomass and force them to bury themselves more shallowly, thus increasing their risk of being depredated. Beyond measuring bivalves grown in artificial clinical conditions, this is a source of error that would be hard to eliminate. Furthermore, the overall size of the siphons taken, not just in length, would have varied because they were unlikely to be complete. Intake rates of intact *Cyclomactra* would be subject to a similar degree of error given that many times the bivalves were consumed by godwits as fragments without shells. In these cases, the largest fragment was measured and its mass estimated, but this would underestimate the overall intake rate of bivalve biomass.

The consumption of flounder was unexpected until birds were observed chasing them through shallow puddles. Dabbling behaviour first became apparent in birds that were hunting flounder as they would stir up water in puddles with their bill and then chase whatever they disturbed. I used a similar technique to capture flounder by hand for measurement. The relationship between flounder capture and foraging by dabbling was supported in the models as dabbling had a positive effect, increasing the likelihood that flounder would be eaten. Sewing behaviour, on the other hand, significantly decreased the likelihood that flounder would be eaten at all, with a much greater negative effect than the positive effect of dabbling. The scale of this effect is likely to be the reason the model containing sewing was the model with the most evidence to support it according to Bayes Factors (Jarosz & Wiley 2014). The negative effect of sewing on flounder intakes is intuitive given the low searching speed of sewing behaviour and the high mobility of flounder. Average depth was found to slightly decrease the likelihood of flounder intake as they were generally surface prey, but this effect was far smaller than that of any foraging mode.

The last prey item taken was the larger *Amphibola* snail, for which no factor had an effect on intakes except decreasing their time spent sewing. The less time a bird spent foraging by sewing increased the likelihood they would ingest one of these snails. While common and visible on the mudflats, these mud snails were at much lower density than the smaller *Potamopyrgus* snails and were very visible so did not need to be discovered using tactile sewing strategies. Dabbling appeared to have no effect as some birds would encounter one and take the opportunity to eat it, however given that they were stationary prey items the intensive dabbling motion was likely not needed. Interestingly, visual foraging did not have any effect on the intake of these larger snails. Throughout the videos they were only taken occasionally despite their prevalence, suggesting perhaps that they were just taken randomly, except for in small birds who did not take them at all.

It must be noted in the preceding discussion, all comments on density of prey items are based on relative quantities of each prey type that appeared in the benthos sampling, the size-mass relationship results of which are supplied in Appendix 2. Patterns in the spatial distribution of prey items, and their densities across the mudflats, were not the subject of this analysis. Further observations of godwit foraging, if combined with more detailed substrate sampling, would enable development of a broader picture of seasonal variation in the distributions and relative abundance of benthic prey, and how godwits respond to these changes. Assessment of seasonal effects on godwit intake rates of the various prey items was not analysed in any detail here because of the relatively short (8 week) observation period that supplied the data used in this study.

Specialisation and individuality

Evidence is mounting to suggest that individual variation plays a significant role in the functional ecology of species (Bolnick *et al.* 2003). I have demonstrated in this thesis that this occurs in the study population of godwits since there were patterns of consumption of prey types that could not be accounted for by factors such as sex or morphology, nor by the environmental factors that were included in the models. The presence of specialist birds with no obvious pattern to what drives them to be specialists is very noticeable in the data. Eight out of 15 males had highly specialised diets and their bill lengths spanned the full range of those in the sample of males in this population. The only obvious pattern was that it was males that tended to specialise (in contrast, only one female was a specialist). Why this is the case is unknown, but this could be due in part to males being more limited in their diet choice because of their shorter bills making deeper prey inaccessible. Simply by being limited in potential probe depth, males are left with fewer options and so develop proficiency in or preference for consuming a particular prey item. Why only certain individuals do this is not known, especially given that the intake rates of specialists are no different to those of individuals with broader diets. In addition to the obvious specialists, more uncommon prey types did not appear to be taken randomly across all birds. Instead, certain birds repeatedly took prey types such as flounders and *Amphibola*, but there was no pattern with regard to their bill lengths. These individuals had broader diets than the specialists, but only some of the generalists capitalised on these prey types. It is possible that there is an ontogenetic component to this behaviour. When birds first arrive as juveniles they are known to explore widely around New Zealand before settling on a non-breeding site (Battley *et al.* 2011). This could result in different birds having different experiences as their learning likely depends upon where they 'sampled'. Young birds are known to not be particularly proficient at foraging (Weathers & Sullivan 1989; Hand *et al.* 2010) but they do gradually improve with experience (Hanzhao *et al.* 2010). It is possible that experiences and opportunities when birds are young shape behaviours

and preferences that become ingrained as adults, and explain the idiosyncratic prey choice of different birds.

Carry-over effects from migration

While no variables influenced diet choice and prey-specific intake rates as much as the chosen foraging mode, one clear pattern was that *Amphibola* were more likely to be taken and in larger quantities the longer a bird has been back from migration. Hard prey like *Amphibola* require physical processing and would be crushed by the muscles in a bird's gizzard to obtain nutrients from them. Migrating birds are known to have decreased digestive tract mass and arrive in this state (Battley *et al.* 2000). Smaller gizzards therefore have neither the space nor the power to process shells adequately. Not only is the gizzard reduced in size, but the rest of the digestive tract is also smaller than normal due to migration. As discussed earlier, this reduction could reduce nutrient assimilation rates and therefore be less efficient for the birds, as is seen in Blackcaps (*Sylvia atricapilla*) at stopover sites. These birds gain little mass in the first three days after arrival (Karasov & Pinshow 2000; Gannes 2002). However, while the trend that birds gradually eat more hard prey is apparent, it is not particularly pronounced, with some birds eating larger prey like mud snails immediately after arrival. Mathot *et al.* (2017) provide a good explanation for this, showing that the diet of Red Knots (*Calidris canutus*) greatly influences the morphology of their gizzard, while the morphology of the gizzard does not play a significant role in the choice of prey. Applied to godwits, this could suggest that birds that choose to eat *Amphibola* will eat them no matter the state of their digestive tract, and such a prey choice would cause their gizzard to recover to a size where it can easily handle such hard prey. The remaining slight trend in intake rates could simply be due to physical digestive limitations as discussed by van Gils *et al.* (2003) as newly arrived birds simply may not have the power to process many snails despite choosing to eat them. *Potamopyrgus*, on the other hand, while being a shelled prey, are so small that they require very little processing force and so likely can be eaten at any time during a bird's recovery.

Future research

This study provides insight into the heterogeneity of Bar-tailed Godwit foraging resulting from morphology and environmental factors. The results illustrate the foraging patterns of these godwits in terms of both diet choice and intake rates. However, limitations of this study are apparent and future studies may address these. Perhaps the biggest limitation of this study is that all of the videos were recorded during the day, and represent only a snapshot of a bird's overall foraging with only one video used per bird per day. The latter was an intentional decision in order to ensure independence

of data points. It would have been possible to have analysed more videos per bird, but only by reducing the number of individuals in the study. As it is, the overall sample size in this study of 34 birds videoed 215 times is adequate and successfully covers a wide range of foraging variation in the birds. Videoing only during the day may potentially miss an important period of foraging for these birds. Nocturnal foraging is known to occur across a number of shorebird species (Dodd & Colwell 1998) and occurs particularly when birds have not met their energy requirements during the day (Santiago-Quesada *et al.* 2014). Nocturnal foraging bouts would be impossible to study with the methods used here but may be important to consider to further our understanding of godwit foraging. Given that one of the major foraging modes used was visual foraging, this is unlikely to be particularly functional at night so there may be a difference in the success of birds where those foraging by tactile means manage to consume more food.

This study also did not investigate whether males and females select different foraging zones, so a future study could examine the spatial distribution of godwits across the mudflats. Morphological differences between sexes are known to result in spatial distribution variation in both Bar-tailed (Duijns *et al.* 2014) and Black-tailed Godwits (*Limosa limosa*) (Catry *et al.* 2012). Zharikov and Skilleter (2002) found that godwits in Australia had notable sex-specific differences in spatial distribution, with males foraging almost entirely in seagrass habitat while the females used both sandy and seagrass habitats equally. However, Alves *et al.* (2013) found no large-scale spatial variation between the sexes of Black-tailed Godwits, which is similar to my observations here, with all of the birds foraging on the same mudflats. Instead, Alves *et al.* (2013) suggested that the segregation was in diet choice, as shown here, with the smaller-billed males taking different prey to longer-billed females. A study of spatial distribution might still be of value in the Manawatu context given the availability of upstream habitats that were not included in this study, and given that within-estuary habitat segregation has also been documented previously (Catry *et al.* 2012). A potential issue with a study such as this would be that only banded birds could be identified reliably given the spectrum of bill lengths present in the population, unless remnants of breeding plumage were still visible. In this study, there was no overlap in bill lengths between males and females, with the largest male having a 91 mm bill and the smallest female having a 95 mm bill. However, the population is known to have overlap in bill length between sexes and so distinguishing the sexes of birds with intermediate sized bills would be difficult (P.F. Battley, 2018, unpub. data). Such was the issue faced by Pierre (1994), where only noticeably male or female birds were used, entirely excluding intermediate birds.

Alongside these analyses of spatial distribution and use of the mudflats, density of birds could be taken into account in a future study. In several videos, godwits were observed attacking or displacing one another. Dominance hierarchies based on size or age are known to influence foraging patterns of

individuals, and female godwits are known to be dominant over males (Catry *et al.* 2012). Interactions between individuals were recorded in the videos but they were not included in the analyses because they did not occur very often, as was the case in Catry *et al.* (2012). Smith and Evans (1973) showed that godwits were more successful when foraging in flocks than when solitary so this might counteract the effects of agonistic behaviour on foraging capacity of godwits. Nevertheless, dominance hierarchies in the nonbreeding godwit population would be an additional avenue to explore to further our understanding of factors that influence godwit foraging patterns.

This study focused on prey choice and intake rates of birds, but more factors could be added in future studies. Faecal analysis was considered during the initial planning phase of the study but, ultimately, was excluded due to time limitations. Faecal analysis is a well-used method for diet studies (Duijns *et al.* 2013; Catry *et al.* 2014; Lourenco *et al.* 2016; Rose *et al.* 2016) and could further help discern the smaller prey items taken by godwits. Video quality was usually adequate for prey identification but smaller prey items that were pulled up from deep in the mud or picked off the surface were assumed to be worm fragments and *Potamopyrgus* respectively, leading to an extra degree of error. These assumptions were likely safe given the relative ease of identifying most other prey items, but faecal analysis could help confirm whether other prey items were present in the diet. For example, amphipods were a particularly common invertebrate collected during benthos sampling but given their size and translucence they would be impossible to identify from videos. If any were taken they would have been coated in mud and therefore looked more like a *Potamopyrgus* but faecal analyses could potentially identify them from undigested fragments (Duijns *et al.* 2013) and provide additional insight into the diet choice of godwits.

While some tests of individuality were conducted in this thesis, more work could be done to explore this. By comparing niche variation across individuals and with respect to the whole population (Ingram *et al.* 2018), a fundamental understanding of the extent of individual specialization in the population could be obtained. In the data presented here, it was clear that individuality did play a role as some birds specialized exclusively on one prey type and less-commonly taken prey items were generally taken by only a subset of individuals. These patterns indicate the influence of individuality on godwit foraging, and clearly show the need for a future study further detailing this influence. Such a study could also examine the occurrence of individuality in recovery patterns of birds as gizzard mass and how this can change is known to vary on an individual by individual basis (Mathot *et al.* 2017). Such a study would require multiple seasons of work to ascertain consistency of individuals, meaning that it is well beyond the scope of this thesis. Despite this, these birds are highly site faithful as adults (Battley *et al.* 2011), so such a study would not be impractical on Bar-tailed Godwits and would vastly improve our understanding of their foraging ecology.

The ontogeny of foraging behaviour would be a particularly interesting future study. Juvenile Bar-tailed Godwits are known to continue bill growth well after fledging (Battley & Conklin 2010), and this is likely to play a role in the development of an individual's foraging proficiency on the non-breeding grounds. One way to determine the effect of this would be to capture and mark juveniles when they arrive in New Zealand and changes in their feeding behaviour across years, both in relation to the bill length of the individual as it grows but also as the bird learns more and encounters more prey types before settling at a 'wintering' site. If combined with remote tracking, it could even be possible to study the same individuals as they sample different sites and habitats.

Another aspect that was not investigated was that of nutrient assimilation. As shown by Gannes (2002) and Karasov and Pinshow (2000), there appear to be limitations on how birds can assimilate their food when they have reduced organ mass. The biggest reductions of mass do not occur in the gizzard, but in assimilation organs such as the small intestine and liver (Bauchinger & McWilliams 2012). The increase of hard-shelled prey in the diet over time alludes to an initial deficit in physical processing capacity by the gizzard, but assessment of assimilation capacity was not part of this study. This would be important to study as godwits could show little impairment of intake rates yet have poor assimilation rates resulting in lower nutrient gain for their efforts. The change over time could instead occur in the efficiency of digestion and how much energy a bird can obtain from their food. Studies of mass changes in birds recovering from migration could provide an estimate of just how long it takes before birds are back to their full rate of assimilation and therefore digestive tract functionality, though the propensity of godwits to stress during handling would make them a poor candidate for captive studies in New Zealand.

Lastly, the influence of age was initially planned to be included in this thesis but was not pursued and could be incorporated into further studies. Studying the foraging and recovery of juvenile birds in comparison to the adults would be of value because juveniles routinely arrive later than most adults in New Zealand (P.F. Battley, pers. comm.). As a result, they might forage on different prey given their later arrival time, the fact they will be recovering from their first ever migration, and their lack of experience with capturing and processing the prey types on offer. It was noticeable in spring 2015, when unusually large numbers of juveniles were present at the Manawatu River Estuary, that juveniles would routinely forage for crabs over the high-tide period when water flooded a saltmarsh area, while adults would roost just a few hundred metres away (P. F. Battley and T. A. Ross, pers. obs.). This could be because juveniles were inefficient at foraging on alternative prey on the tidal flats, so needed to supplement their intakes with crabs, but this needs to be tested by further studies. As no juveniles arrive already banded, individual recognition is impossible but cohort-level comparisons (juveniles versus adults, including sex differences) could still be possible.

Bar-tailed Godwits clearly exhibit some significant patterns of variation in their diet. Due to such a wide range in foraging morphology, birds of different bill lengths have access to different prey types with the longer-billed females having the widest range of diet options of the species. Instead of all foraging the same way, godwits exhibit prey-specific foraging modes by which shorter-billed birds (males) target different prey items and manage to maintain higher intakes than the longer-billed birds (females). By targeting different prey items, the shorter-billed males manage to ameliorate the disparity in prey availability they would otherwise face. Furthermore, birds clearly experience some recovery period over the first few days upon arriving from migration where they slowly increase their intake rates. However, these effects are very minor and are likely due to the space available in a bird's digestive tract, as very few temporal patterns in prey selection are visible beyond the hardest shelled prey items. The Manawatu Estuary provides a variable prey range including soft, small prey types so foraging godwits can maintain intake rates while also consuming prey items that enable their gut to regain full functionality required to process a full diet. This diversity in prey options may be a key feature of the habitat that allows godwits to successfully complete the longest-distance migratory flight known of any bird.

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Appendix 1: Birds filmed in the study.

Asterisks denote videos taken on days relative to arrival date (where 0 equals the arrival date). Birds are ordered by bill length (smallest to largest).

<i>Bird</i>	<i>Bill (mm)</i>	<i>Sex</i>	<i>Banded</i>	<i>Arrival date '17</i>	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
6WRWY	73	m	Nov-14	18 Sep			*		*					*	*		*			
BHR	75	m	Nov-13	17 Sep	*	*														
BEP	78	m	Nov-14	8 Sep	*	*	*			*	*	*	*	*	*	*				
4YRBB	80.1	m	Feb-07	18 Sep	*	*									*			*		
6WRRB	81	m	Nov-14	1 Oct	*	*												*	*	
6WRWB	82	m	Nov-14	15 Sep	*	*						*						*		
AJD	83	m	Oct-08	17 Sep	*	*											*	*		
6YYBW	83.4	m	Nov-10	8 Sep		*	*	*	*	*	*	*		*	*	*				
6WBY Y	83.7	m	Mar-17	2 Oct		*	*	*	*					*						*
4YYRB	84.7	m	Feb-06	7 Sep	*	*						*	*	*	*	*				
6YWWB	85.7	m	Nov-12	5 Sep	*	*			*	*	*	*	*	*	*	*			*	
6WRBB	87	m	Nov-14	14 Sep	*	*	*	*		*										
6WRWR	89	m	Nov-14	18 Sep		*			*				*	*	*	*				
6WBYR	90	m	Mar-17	5 Sep	*	*		*	*	*	*	*				*				
6RWBY	91	m	Nov-13	11 Sep	*		*	*	*	*	*	*				*				
6YYWR	95.2	f	Nov-10	9 Oct	*				*	*										
4YYYY	104.8	f	Jan-06	8 Sep	*	*	*	*	*											
6RWBW	105	f	Nov-13	15 Sep	*				*			*								
6RWRB	106	f	Nov-13	9 Sep	*				*	*	*									
BEU	106	f	Nov-14	8 Sep	*	*		*				*	*	*	*					
6RWRR	107	f	Feb-13	9 Oct		*		*	*						*	*				
AMT	108	f	Oct-08	2 Oct	*							*		*		*		*	*	
6RWY Y	110	f	Feb-13	15 Sep	*				*			*			*					*
AMV	111	f	Oct-08	7 Sep	*	*		*	*	*	*	*		*			*			
BET	111	f	Nov-14	7 Sep		*	*	*	*	*	*	*	*	*			*	*		
4YWRB	113.9	f	Feb-06	8 Sep	*	*		*	*	*	*					*	*			
6YWWY	114	f	Nov-13	7 Sep		*	*		*	*		*	*	*	*	*	*			*
6RYWR	115	f	Feb-13	8 Sep			*	*	*		*	*		*		*				
6YBRB	116	f	Mar-08	10 Sep	*		*		*	*	*			*					*	
6YRWY	116	f	Nov-13	7 Sep		*	*		*											*
4YYBR	117.8	f	Feb-06	4 Sep		*	*					*	*	*	*		*	*		*
6RRBB	119.5	f	Jan-14	14 Sep	*								*							
4YRYB	121	f	Sep-06	8 Sep	*	*	*	*		*	*	*	*							
4YRWB*	125	f	Nov-09	14 Sep	*				*	*					*	*	*		*	

*4YRWB was also filmed on the 19th day since arrival.

Appendix 2: Benthos sampling models

The plots and relationships shown below are those derived from benthos data and used to estimate prey item AFDM from videography. Individuals were often combined into size classes, e.g. in worms where worms were divided into 10mm size classes.

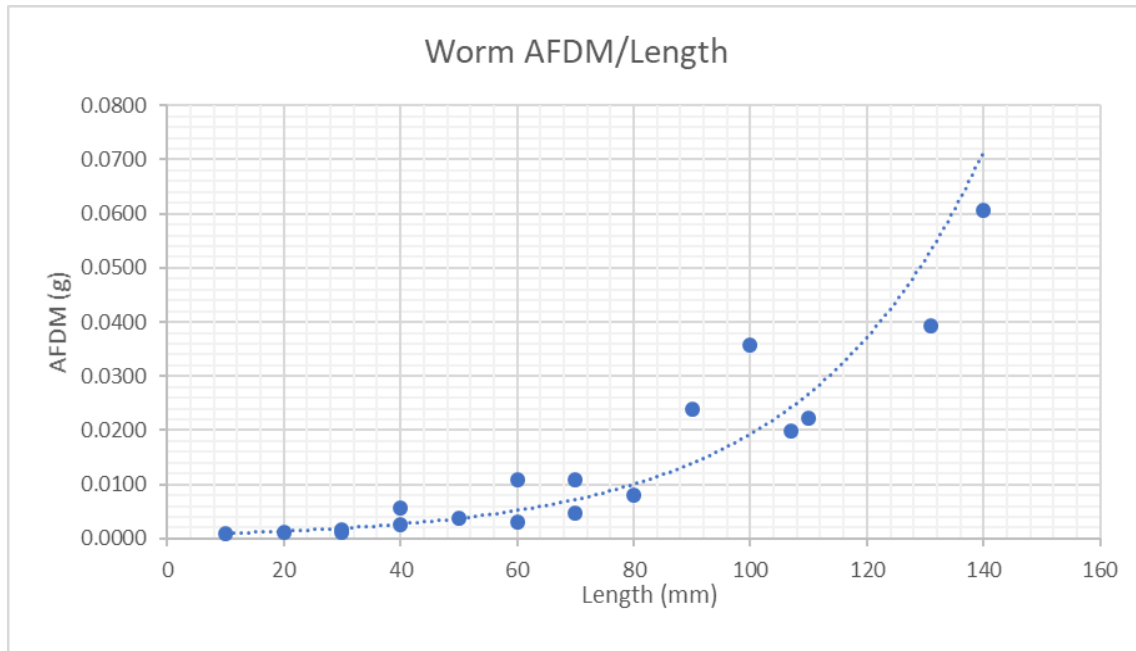


Figure 1: Length-mass relationship for worms, n= 56. Equation: $y = 0.0007e^{0.0328x}$, $R^2 = 0.8998$.

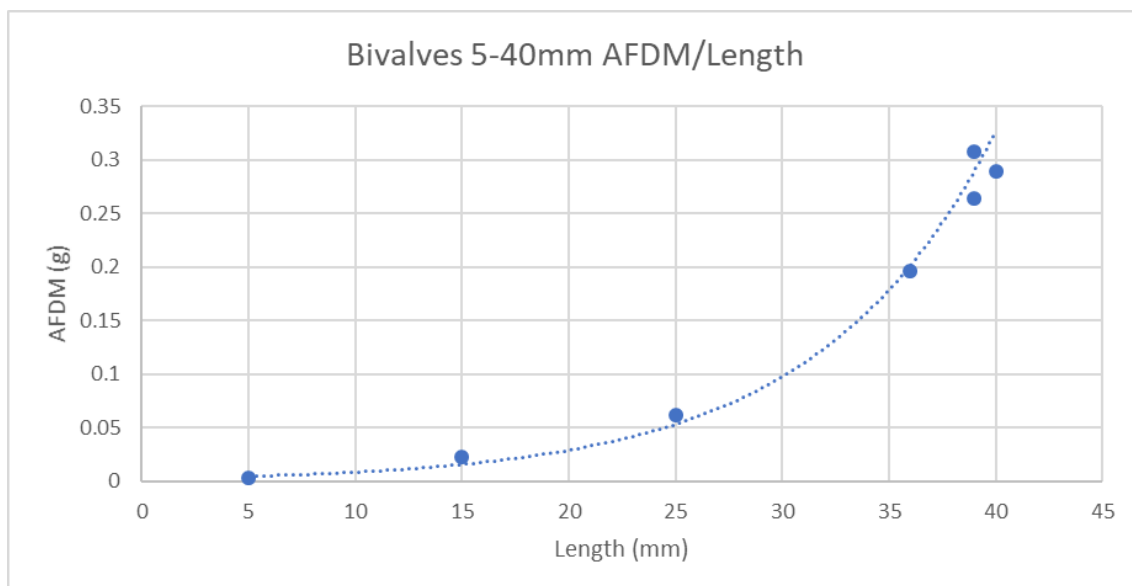


Figure 2: Length-mass relationship for *Cyclomactra* bivalves, n= 22. Equation: $y = 0.0026e^{0.1208x}$, $R^2 = 0.9840$.

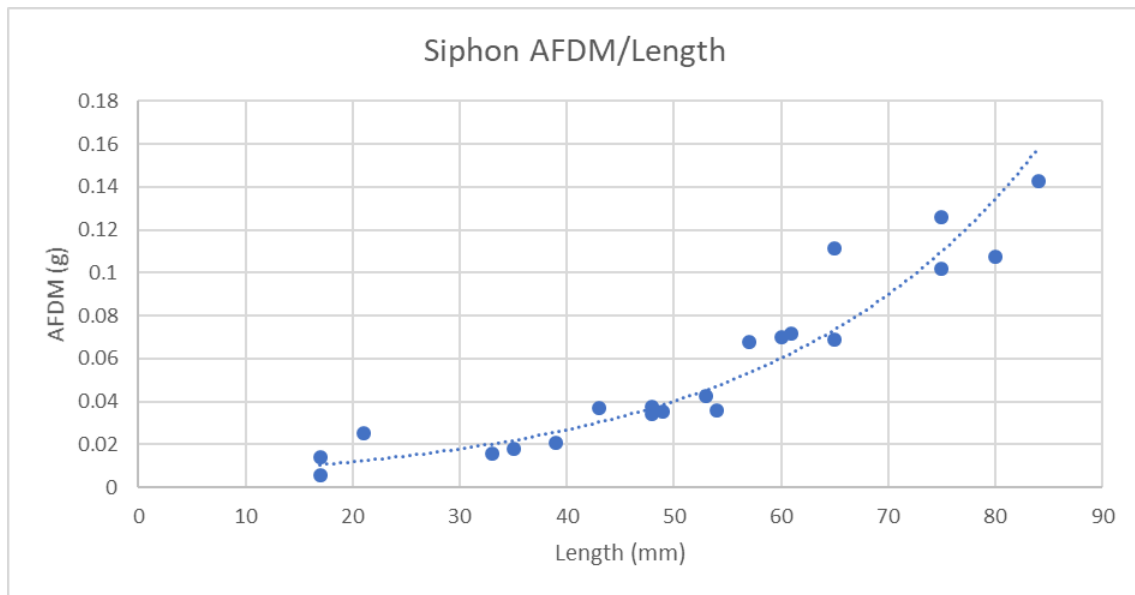


Figure 3: Length-mass relationship for siphons, n= 21. Equation: $y = 0.0054e^{0.0402x}$, $R^2 = 0.8846$.

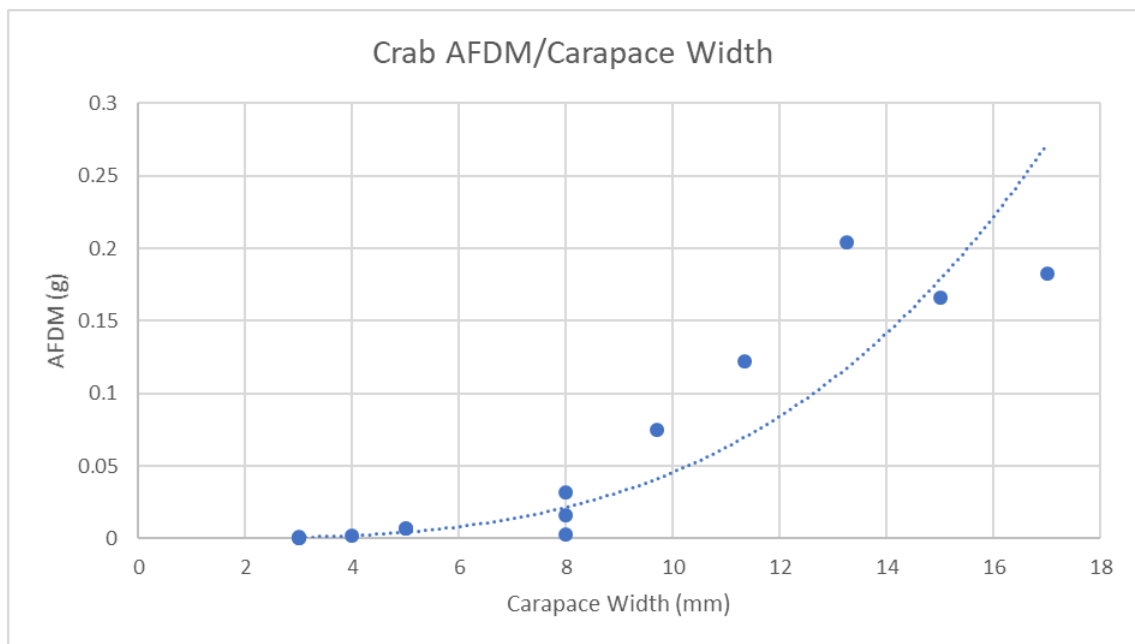


Figure 4: Length-mass relationship for crabs, n= 17. Equation: $y = 2E-05x^{3.3648}$, $R^2 = 0.9033$.

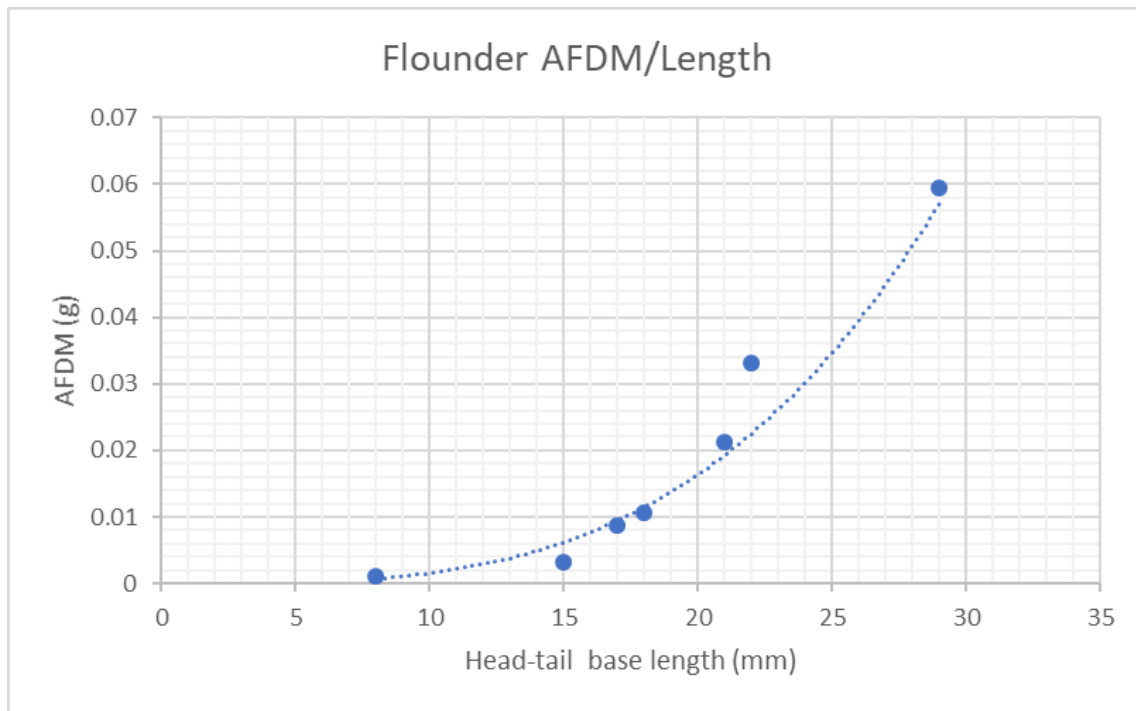


Figure 5: Length-mass relationship for flounders, n= 7. Equation: $y = 7E-07x^{3.3673}$, $R^2 = 0.9411$.

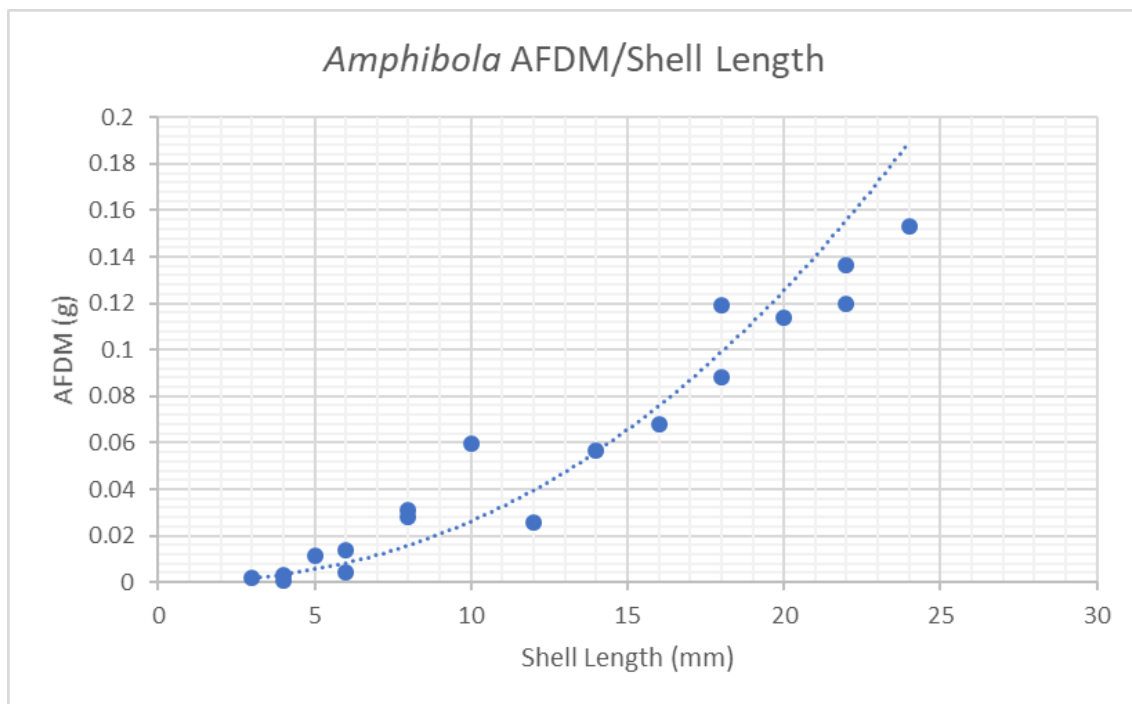


Figure 6: Length-mass relationship for *Amphibola* mud snails, n= 104. Equation: $y = 0.0001x^{2.2588}$, $R^2 = 0.8917$.

Appendix 3: Specialist vs. generalist feeders

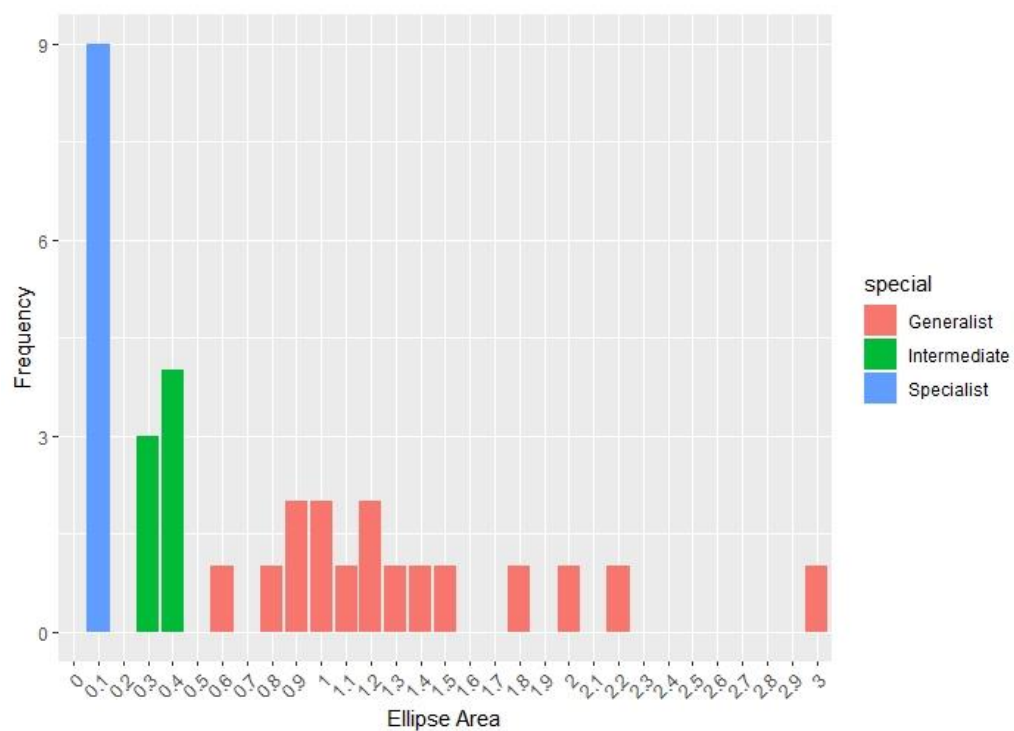


Figure 1: Frequency of ellipse areas for the 32 birds with 3 or more observations. Birds with areas <0.1 units were considered to be specialists, those between 0.1 and 0.4 as intermediate and those above 0.4 as generalist birds.

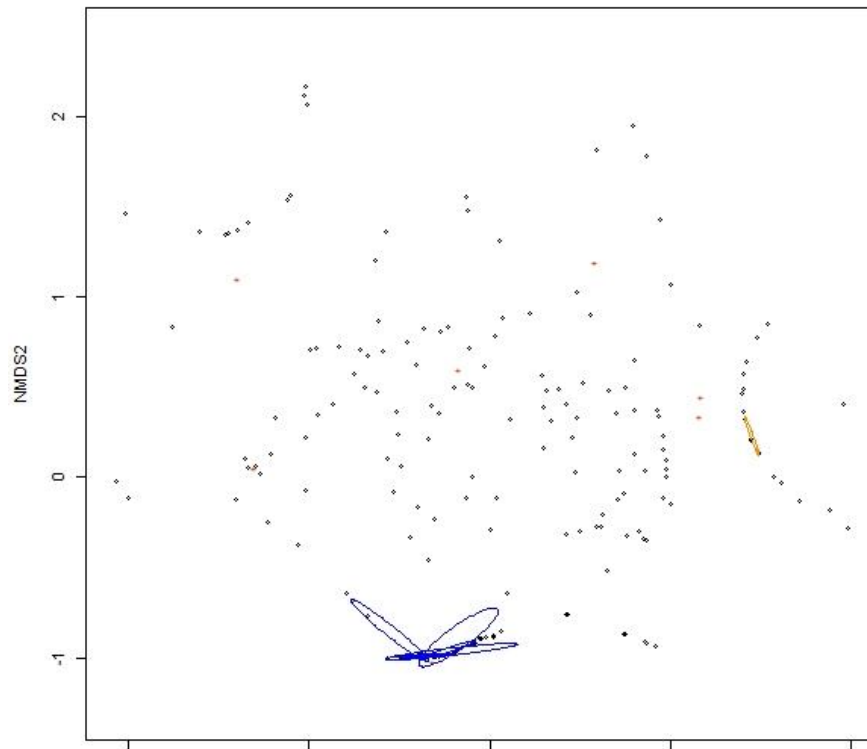


Figure 2: Ellipses of specialist bird foraging bouts (ellipse area <0.1 units), n= 9.

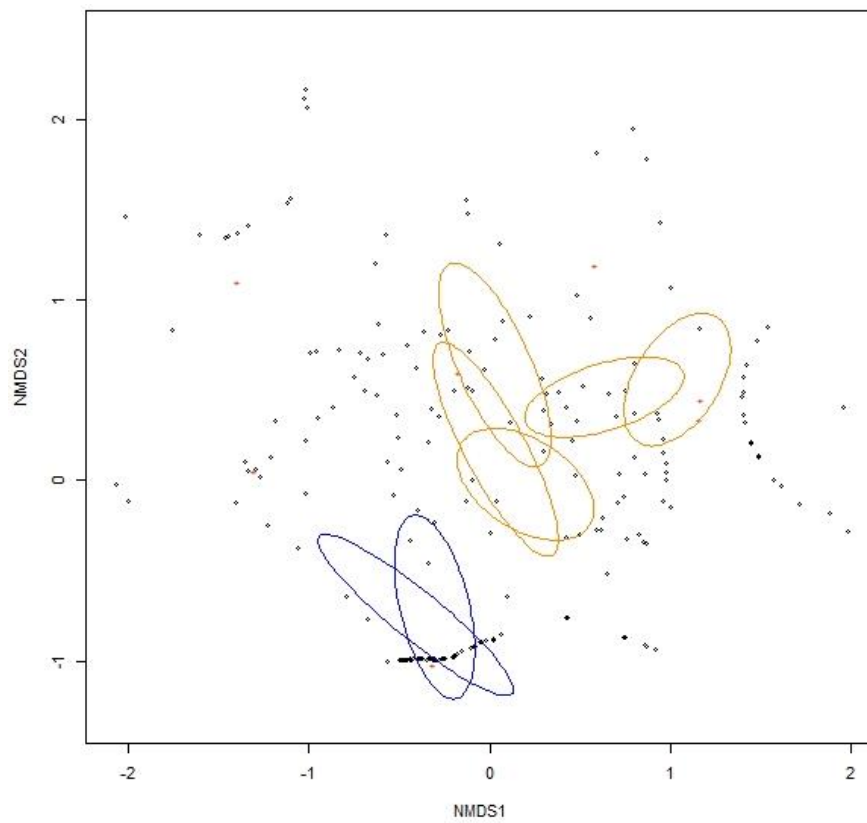


Figure 3: Ellipses of intermediate bird foraging bouts (Area 0.1-0.4 units), n= 7.

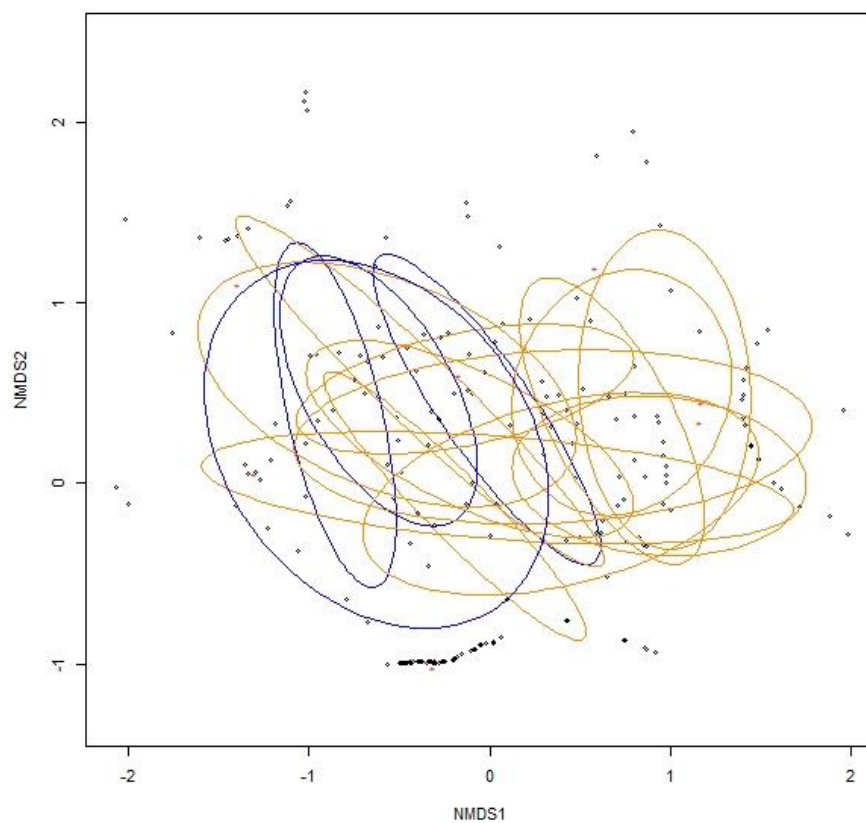


Figure 4: Ellipses of generalist bird foraging bouts (Area >0.4 units), n= 16.

Appendix 4: Prey intake rates per individual

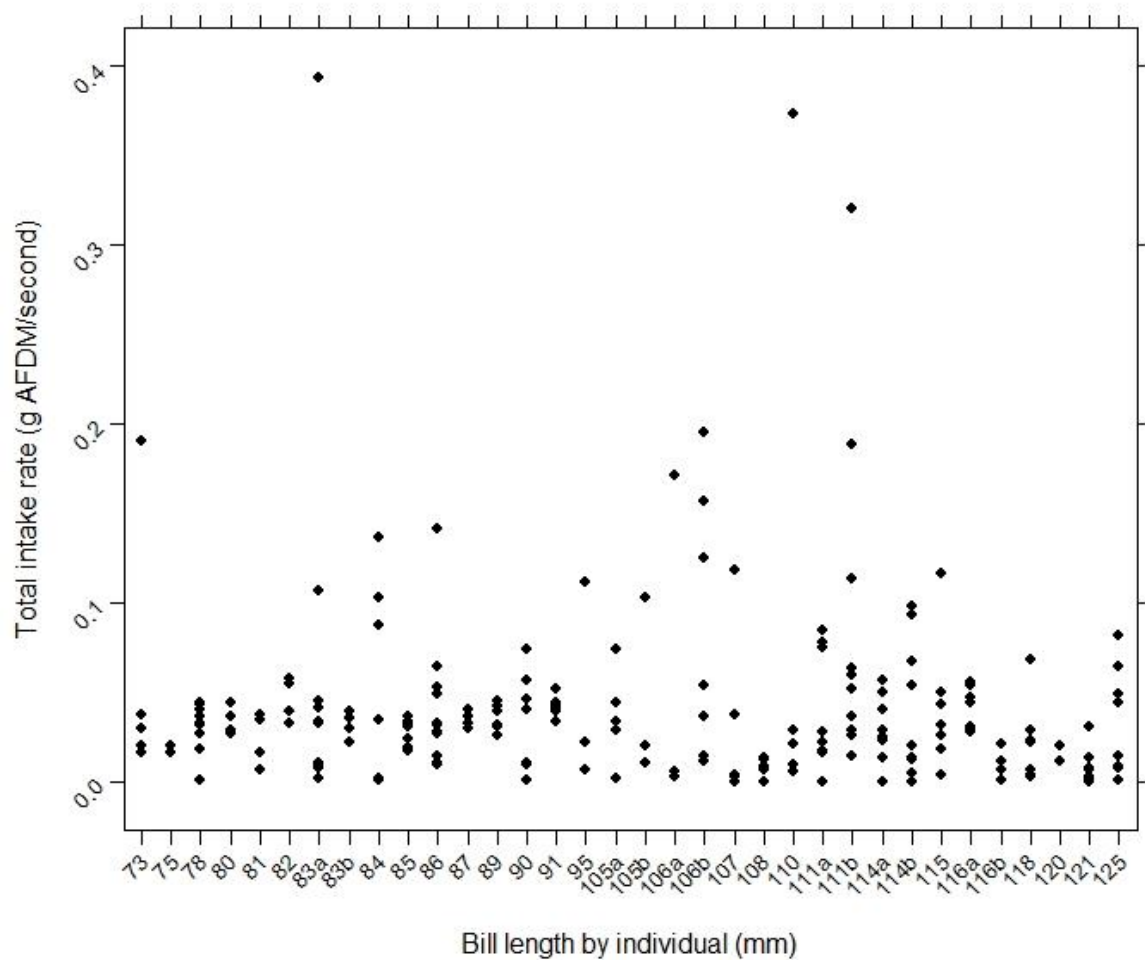


Figure 1: Overall intake rates per individual bird. Birds with the same bill lengths are shown as a and b.

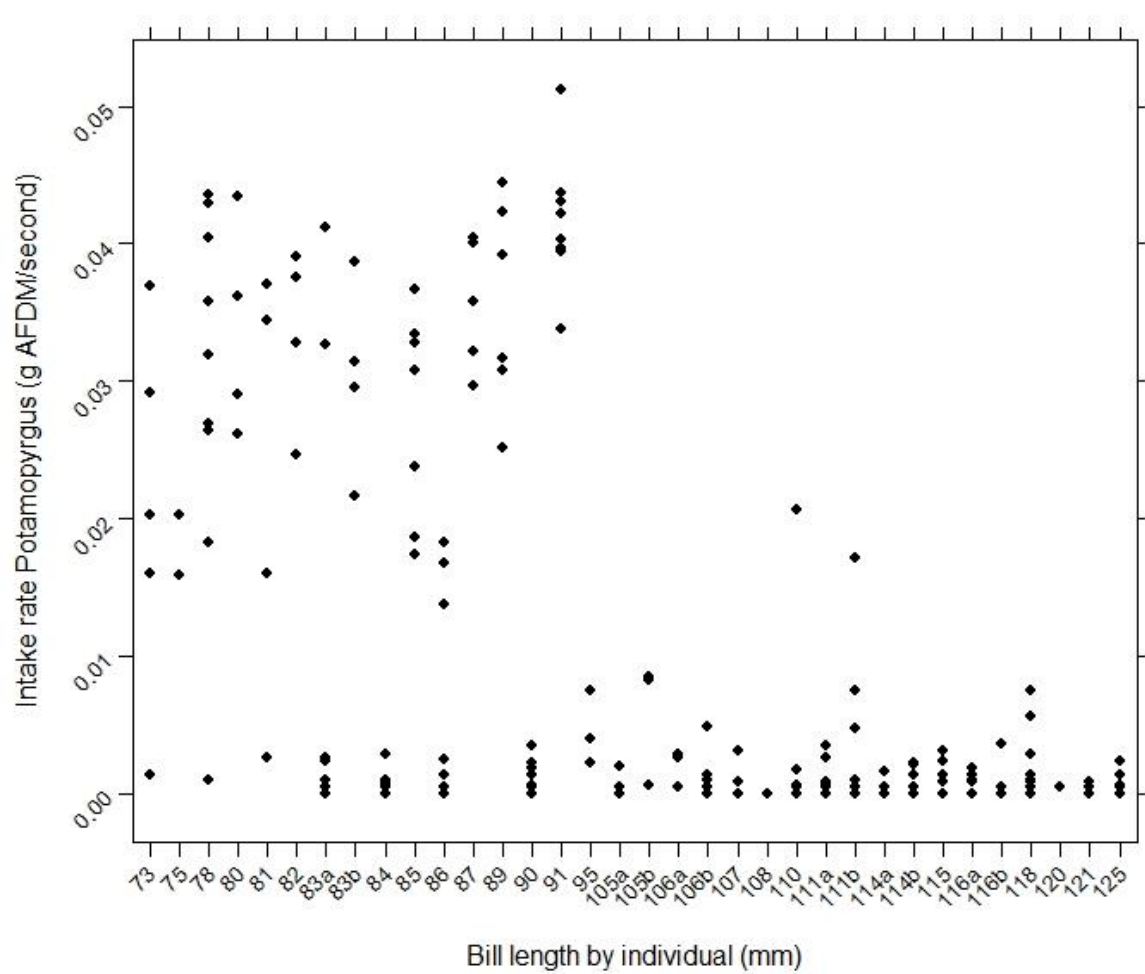


Figure 2: Intake rates of *Potamopyrgus* per individual bird.

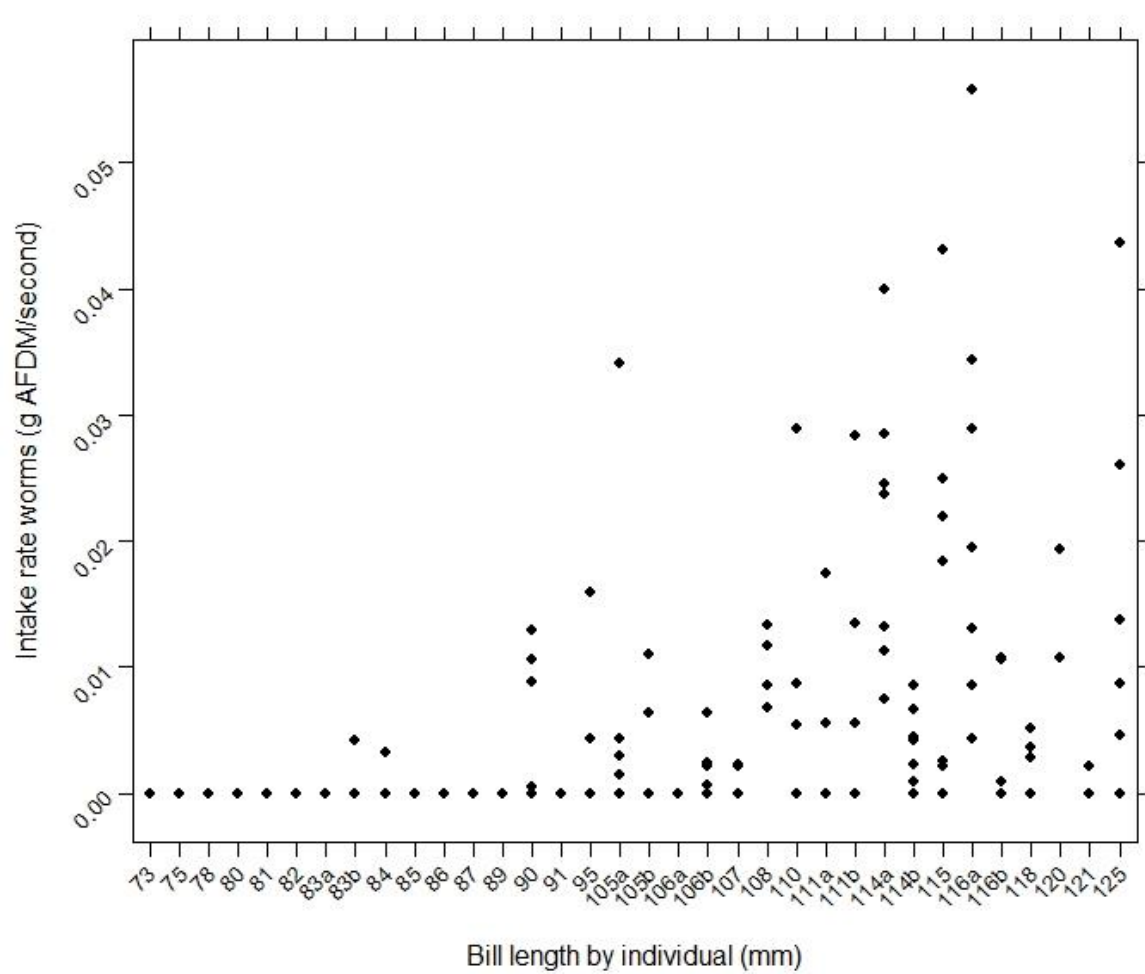


Figure 3: Intake rates of worms per individual bird.

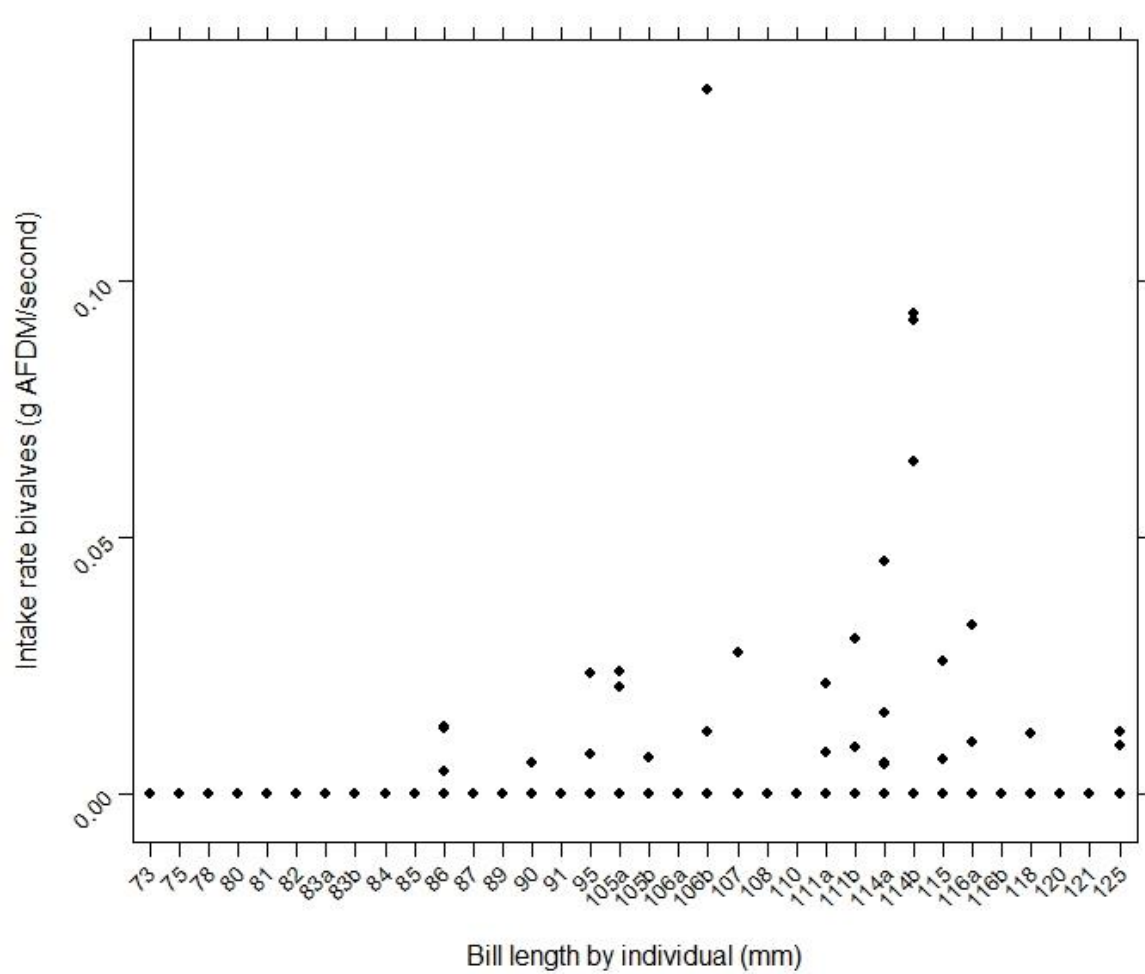


Figure 4: Intake rates of *Cyclomactra* bivalves per individual bird.

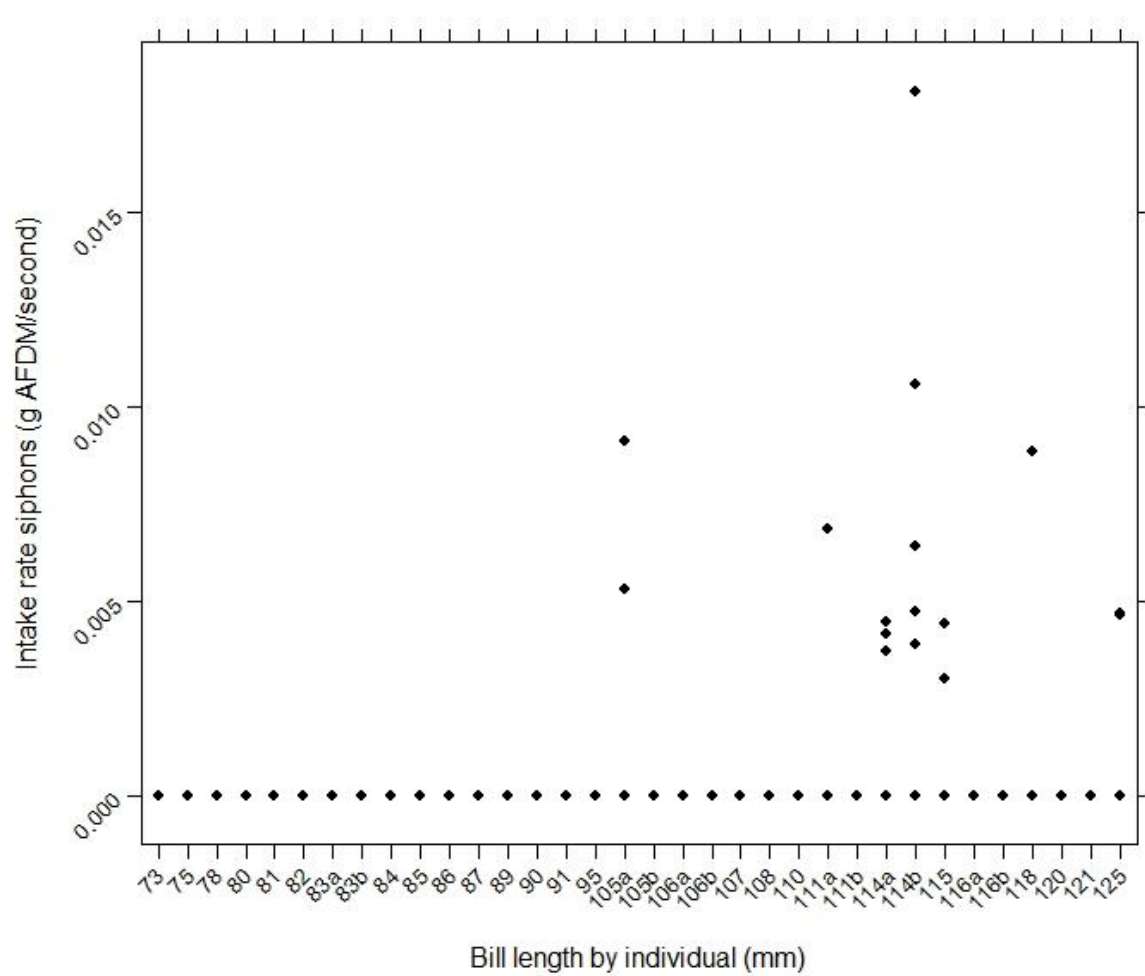


Figure 5: Intake rates of *Cyclomactra* siphons per individual bird.

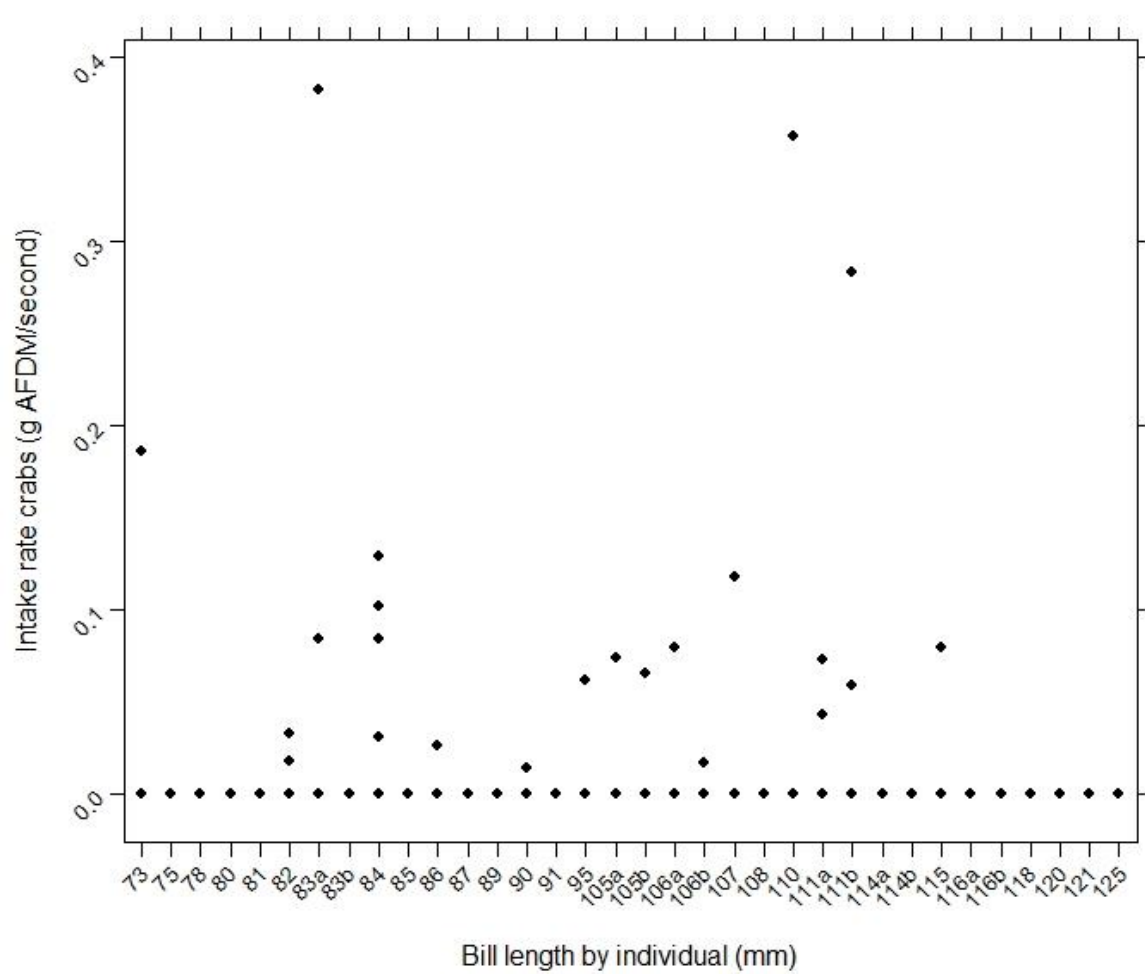


Figure 6: Intake rates of crabs per individual bird.

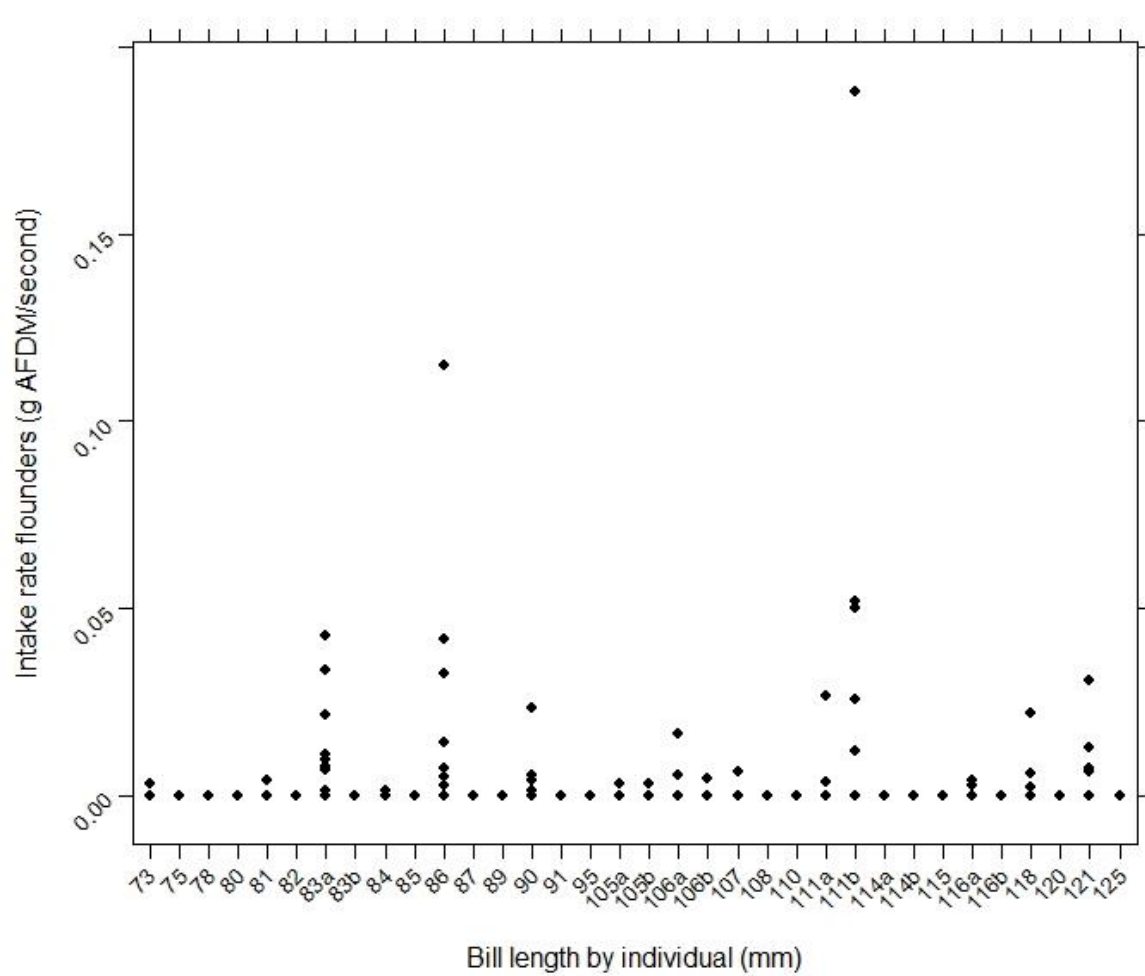


Figure 7: Intake rates of *Rhombosolea* sp. flounders per individual bird.

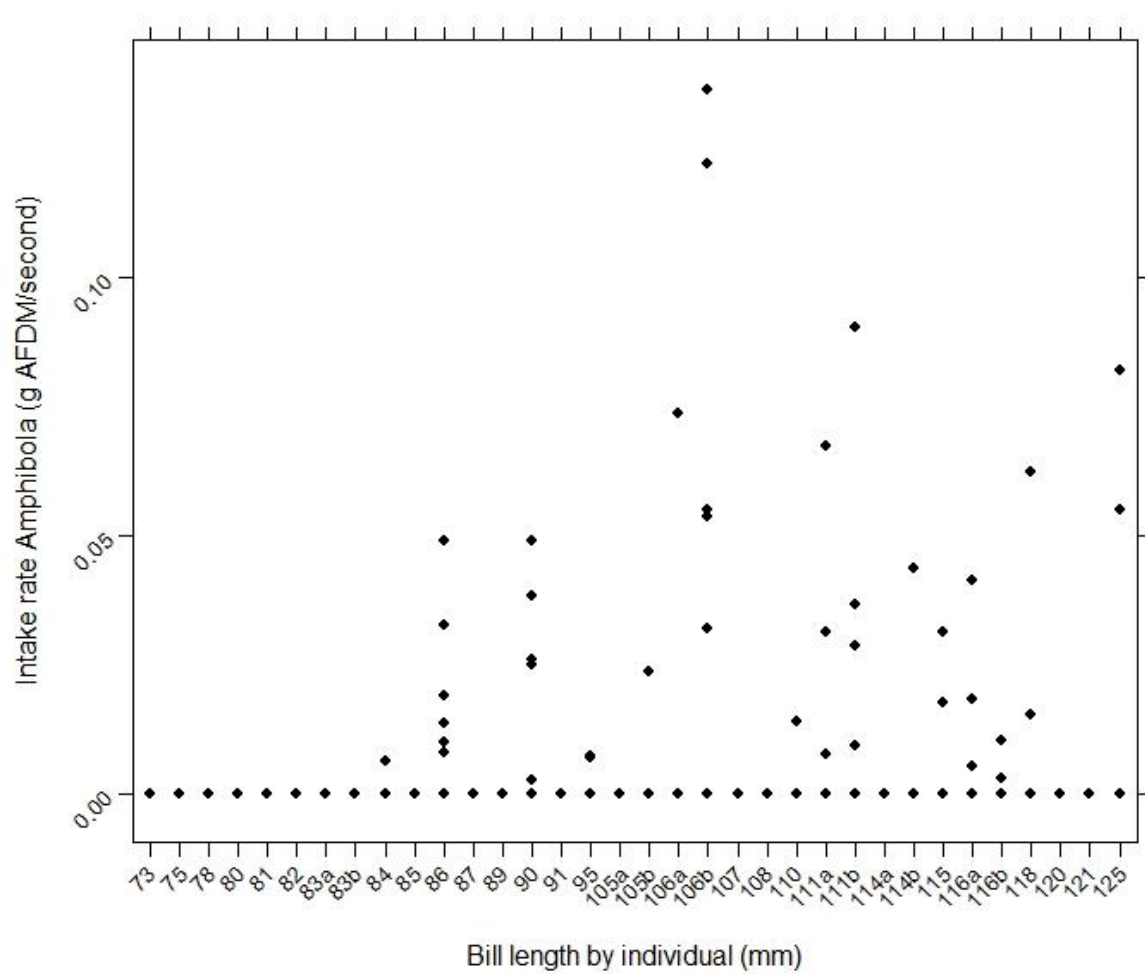


Figure 8: Intake rates of *Amphibola* mud snails per individual bird.

Appendix 5: Full log-normal hurdle model outputs

The model outputs included below (Figures 1-7) are only those selected and summarised in Chapter 2.

Variables:

Bill:

pace.tot: Total pacing rate/searching speed in the video.

ttlt:altTRUE: Time relative to low tide, shown as an interaction between **ttlt** (absolute value of minutes since low tide) and **altTRUE** (whether the video was taken before or after low tide)

ave.depth: average depth to which the bird probed in the video.

prop.sew/vis: proportion of time spent sewing or visually foraging.

hu_: Prefix denoting the hurdle estimates of the model (likelihood of whether prey taken at all).

```
> summary(potsewB)
Family: hurdle_lognormal
Links: mu = identity; sigma = identity; hu = logit
Formula: rate.su ~ bill + pace.tot + ttlt * alt + prop.sew + (1 | bird)
         hu ~ bill + pace.tot + ttlt * alt + prop.sew + (1 | bird)
Data: data (Number of observations: 215)
Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
         total post-warmup samples = 4000
```

Group-Level Effects:

~bird (Number of levels: 34)

	Estimate	Est.Error	l-95% CI	u-95% CI	Eff.Sample	Rhat
sd(Intercept)	0.17	0.10	0.01	0.39	1146	1.00
sd(hu_Intercept)	0.87	0.40	0.13	1.74	1148	1.00

Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Eff.Sample	Rhat
Intercept	-4.86	0.67	-6.18	-3.51	4611	1.00
hu_Intercept	-6.02	2.57	-11.60	-1.38	2710	1.00
bill	-0.02	0.01	-0.03	-0.00	5527	1.00
pace.tot	-0.08	0.12	-0.31	0.15	5434	1.00
ttlt	-0.00	0.00	-0.00	0.00	4494	1.00
altTRUE	-0.03	0.24	-0.47	0.45	5466	1.00
prop.sew	2.82	0.24	2.35	3.29	3874	1.00
ttlt:altTRUE	0.00	0.00	-0.00	0.01	5080	1.00
hu_bill	0.03	0.02	-0.01	0.08	2939	1.00
hu_pace.tot	0.48	0.30	-0.09	1.10	5799	1.00
hu_ttlt	0.00	0.00	-0.01	0.01	3752	1.00
hu_altTRUE	1.14	0.78	-0.31	2.73	3395	1.00
hu_prop.sew	-3.46	1.77	-7.53	-0.61	3053	1.00
hu_ttlt:altTRUE	-0.01	0.01	-0.02	0.00	3555	1.00

Family Specific Parameters:

	Estimate	Est.Error	l-95% CI	u-95% CI	Eff.Sample	Rhat
sigma	0.78	0.05	0.69	0.88	3716	1.00

Samples were drawn using sampling(NUTS). For each parameter, Eff.Sample is a crude measure of effective sample size, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

Figure 1: Log-normal hurdle model of *Potamopyrgus* intake rates.

```
> summary(wormvisB)
Family: hurdle_lognormal
Links: mu = identity; sigma = identity; hu = logit
Formula: rate.allworm ~ bill + pace.tot + ttlt * alt + prop.vis + (1 | bird)
         hu ~ bill + pace.tot + ttlt * alt + prop.vis + (1 | bird)
Data: data (Number of observations: 215)
Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
         total post-warmup samples = 4000
```

Group-Level Effects:

~bird (Number of levels: 34)

	Estimate	Est.Error	l-95% CI	u-95% CI	Eff.Sample	Rhat
sd(Intercept)	0.50	0.18	0.17	0.88	1396	1.00
sd(hu_Intercept)	1.63	0.52	0.75	2.83	1523	1.00

Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Eff.Sample	Rhat
Intercept	-8.93	1.92	-12.72	-5.02	4295	1.00
hu_Intercept	12.17	3.65	5.94	20.16	2524	1.00
bill	0.04	0.02	-0.00	0.07	4430	1.00
pace.tot	-0.39	0.23	-0.82	0.08	4364	1.00
ttlt	0.01	0.00	0.00	0.01	4604	1.00
altTRUE	0.27	0.50	-0.69	1.26	4147	1.00
prop.vis	0.63	0.59	-0.55	1.77	3864	1.00
ttlt:altTRUE	-0.00	0.00	-0.01	0.00	4320	1.00
hu_bill	-0.10	0.04	-0.17	-0.04	2350	1.00
hu_pace.tot	0.55	0.51	-0.45	1.58	3721	1.00
hu_ttlt	0.00	0.01	-0.01	0.02	3464	1.00
hu_altTRUE	-0.58	0.98	-2.52	1.29	3705	1.00
hu_prop.vis	-4.65	1.20	-7.19	-2.50	3666	1.00
hu_ttlt:altTRUE	-0.01	0.01	-0.02	0.01	3262	1.00

Family Specific Parameters:

	Estimate	Est.Error	l-95% CI	u-95% CI	Eff.Sample	Rhat
sigma	0.91	0.09	0.75	1.10	2947	1.00

Samples were drawn using sampling(NUTS). For each parameter, Eff.Sample is a crude measure of effective sample size, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

Figure 2: Log-normal hurdle model of worm intake rates.

```

> summary(bivsewB)
Family: hurdle_lognormal
Links: mu = identity; sigma = identity; hu = logit
Formula: rate.biv ~ ave.depth + pace.tot + ttlt * alt + prop.sew + (1 | bird)
         hu ~ ave.depth + pace.tot + ttlt * alt + prop.sew + (1 | bird)
Data: data (Number of observations: 215)
Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
         total post-warmup samples = 4000

Group-Level Effects:
~bird (Number of levels: 34)
      Estimate Est.Error l-95% CI u-95% CI Eff.Sample Rhat
sd(Intercept)      0.47      0.26      0.04      1.05     1209 1.00
sd(hu_Intercept)    0.51      0.36      0.02      1.36     1427 1.00

Population-Level Effects:
      Estimate Est.Error l-95% CI u-95% CI Eff.Sample Rhat
Intercept      -5.59      0.92     -7.34     -3.78     3666 1.00
hu_Intercept     1.28      1.10     -0.87      3.45     4097 1.00
ave.depth        0.01      0.01     -0.01      0.03     3267 1.00
pace.tot        -0.13      0.29     -0.70      0.42     3175 1.00
ttlt             0.01      0.00     -0.00      0.01     2977 1.00
altTRUE          1.16      0.61     -0.05      2.33     2956 1.00
prop.sew         8.96     57.47    -108.23    121.52     1272 1.00
ttlt:altTRUE     -0.01      0.01     -0.02      0.00     2459 1.00
hu_ave.depth     -0.02      0.01     -0.04     -0.01     5517 1.00
hu_pace.tot       0.43      0.34     -0.22      1.11     4248 1.00
hu_ttlt          0.01      0.01     -0.00      0.02     3246 1.00
hu_altTRUE        1.62      0.86     -0.00      3.29     2959 1.00
hu_prop.sew       8.20      4.74      2.41     20.11     1214 1.00
hu_ttlt:altTRUE  -0.01      0.01     -0.03      0.00     2920 1.00

Family Specific Parameters:
      Estimate Est.Error l-95% CI u-95% CI Eff.Sample Rhat
sigma      0.82      0.16      0.57      1.17     1782 1.00

Samples were drawn using sampling(NUTS). For each parameter, Eff.Sample
is a crude measure of effective sample size, and Rhat is the potential
scale reduction factor on split chains (at convergence, Rhat = 1).

```

Figure 3: Log-normal hurdle model of *Cyclomactra* bivalve intake rates.

```

> summary(siphsewB)
Family: hurdle_lognormal
Links: mu = identity; sigma = identity; hu = logit
Formula: rate.siph ~ ave.depth + pace.tot + ttlt * alt + prop.sew + (1 | bird)
         hu ~ ave.depth + pace.tot + ttlt * alt + prop.sew + (1 | bird)
Data: data (Number of observations: 215)
Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
         total post-warmup samples = 4000

Group-Level Effects:
~bird (Number of levels: 34)
      Estimate Est.Error 1-95% CI u-95% CI Eff.Sample Rhat
sd(Intercept)      0.41      0.31    0.03    1.20      499 1.00
sd(hu_Intercept)   1.77      0.91    0.24    3.83      318 1.02

Population-Level Effects:
      Estimate Est.Error 1-95% CI u-95% CI Eff.Sample Rhat
Intercept      -6.34      1.43   -9.22   -3.62      763 1.00
hu_Intercept    11.02      3.12    5.91   18.16      578 1.01
ave.depth       -0.00      0.02   -0.03    0.03      540 1.00
pace.tot         0.36      0.24   -0.14    0.83      501 1.00
ttlt             0.00      0.00   -0.00    0.01      827 1.00
altTRUE          0.25      0.61   -0.96    1.48      391 1.00
prop.sew         12.62     55.69 -108.08  125.78      466 1.00
ttlt:altTRUE     -0.00      0.00   -0.01    0.00      618 1.00
hu_ave.depth     -0.06      0.03   -0.12   -0.02      626 1.01
hu_pace.tot     -1.22      0.59   -2.49   -0.13      812 1.00
hu_ttlt          0.01      0.01   -0.01    0.03      626 1.00
hu_altTRUE       1.70      1.47   -1.15    4.57      644 1.00
hu_prop.sew      2.46      4.77   -4.46   14.53      274 1.01
hu_ttlt:altTRUE  -0.02      0.01   -0.04    0.00      536 1.00

Family Specific Parameters:
      Estimate Est.Error 1-95% CI u-95% CI Eff.Sample Rhat
sigma      0.46      0.16    0.24    0.85      442 1.00

Samples were drawn using sampling(NUTS). For each parameter, Eff.Sample
is a crude measure of effective sample size, and Rhat is the potential
scale reduction factor on split chains (at convergence, Rhat = 1).

```

Figure 4: Log-normal hurdle model of siphon intake rates.

```

> summary(crabsewA)
Family: hurdle_lognormal
Links: mu = identity; sigma = identity; hu = logit
Formula: rate.crab ~ bill + pace.tot + ttl_t * alt + prop.sew + (1 | bird)
         hu ~ bill + pace.tot + ttl_t * alt + prop.sew + (1 | bird)
Data: data (Number of observations: 215)
Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
         total post-warmup samples = 4000

Group-Level Effects:
~bird (Number of levels: 34)

```

	Estimate	Est.Error	l-95% CI	u-95% CI	Eff.Sample	Rhat
sd(Intercept)	0.61	0.37	0.04	1.43	805	1.00
sd(hu_Intercept)	0.70	0.49	0.03	1.84	1174	1.00

```

Population-Level Effects:

```

	Estimate	Est.Error	l-95% CI	u-95% CI	Eff.Sample	Rhat
Intercept	-3.52	2.39	-8.22	1.12	3324	1.00
hu_Intercept	-5.61	2.57	-10.93	-0.90	3364	1.00
bill	0.01	0.02	-0.04	0.06	3365	1.00
pace.tot	0.14	0.41	-0.68	0.97	3973	1.00
ttl_t	0.00	0.00	-0.01	0.01	3385	1.00
altTRUE	-0.14	0.87	-1.82	1.57	3015	1.00
prop.sew	-0.72	1.42	-3.48	2.19	3003	1.00
ttl_t:altTRUE	-0.00	0.01	-0.02	0.01	2676	1.00
hu_bill	0.05	0.02	0.01	0.11	3221	1.00
hu_pace.tot	0.59	0.42	-0.23	1.45	4804	1.00
hu_ttl_t	0.00	0.00	-0.01	0.01	4151	1.00
hu_altTRUE	1.46	0.94	-0.36	3.32	3600	1.00
hu_prop.sew	3.99	1.30	1.70	6.87	3122	1.00
hu_ttl_t:altTRUE	-0.00	0.01	-0.02	0.01	3966	1.00

```

Family Specific Parameters:

```

	Estimate	Est.Error	l-95% CI	u-95% CI	Eff.Sample	Rhat
sigma	0.90	0.24	0.52	1.45	1109	1.00

Samples were drawn using sampling(NUTS). For each parameter, Eff.Sample is a crude measure of effective sample size, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

Figure 5: Log-normal hurdle model of crab intake rates.

```

> summary(flounsewB)
Family: hurdle_lognormal
Links: mu = identity; sigma = identity; hu = logit
Formula: rate.floun ~ ave.depth + pace.tot + ttlt * alt + prop.sew + (1 | bird)
         hu ~ ave.depth + pace.tot + ttlt * alt + prop.sew + (1 | bird)
Data: data (Number of observations: 215)
Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
         total post-warmup samples = 4000

Group-Level Effects:
~bird (Number of levels: 34)
      Estimate Est.Error 1-95% CI u-95% CI Eff.Sample Rhat
sd(Intercept)      0.57    0.29   0.05   1.18    1104 1.00
sd(hu_Intercept)   1.74    0.68   0.60   3.27    1035 1.01

Population-Level Effects:
      Estimate Est.Error 1-95% CI u-95% CI Eff.Sample Rhat
Intercept      -2.81    1.05  -4.93  -0.80    4155 1.00
hu_Intercept    -2.20    1.39  -4.99   0.46    2940 1.00
ave.depth       -0.01    0.00  -0.02   0.00    6011 1.00
pace.tot        -0.48    0.35  -1.18   0.21    5156 1.00
ttlt            -0.00    0.00  -0.01   0.00    3555 1.00
altTRUE         -0.43    0.72  -1.88   1.01    3077 1.00
prop.sew        10.84   57.15 -106.09 129.30    1425 1.00
ttlt:altTRUE     0.00    0.01  -0.01   0.01    3146 1.00
hu_ave.depth     0.03    0.01   0.02   0.05    5654 1.00
hu_pace.tot      0.42    0.42  -0.38   1.26    4716 1.00
hu_ttlt         -0.00    0.01  -0.01   0.01    2745 1.00
hu_altTRUE       1.60    1.15  -0.62   3.90    2220 1.00
hu_prop.sew     10.38    4.34   4.18  20.74    1645 1.00
hu_ttlt:altTRUE  -0.00    0.01  -0.02   0.01    2541 1.00

Family Specific Parameters:
      Estimate Est.Error 1-95% CI u-95% CI Eff.Sample Rhat
sigma      1.10    0.15   0.86   1.44    2314 1.00

```

Samples were drawn using sampling(NUTS). For each parameter, Eff.Sample is a crude measure of effective sample size, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

Figure 6: Log-normal hurdle model of flounder intake rates.

```

> summary(snailsewA)
Family: hurdle_lognormal
Links: mu = identity; sigma = identity; hu = logit
Formula: rate.snail ~ bill + pace.tot + ttlt * alt + prop.sew + (1 | bird)
         hu ~ bill + pace.tot + ttlt * alt + prop.sew + (1 | bird)
Data: data (Number of observations: 215)
Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
         total post-warmup samples = 4000

Group-Level Effects:
~bird (Number of levels: 34)

```

	Estimate	Est.Error	l-95% CI	u-95% CI	Eff.Sample	Rhat
sd(Intercept)	0.60	0.25	0.12	1.12	1129	1.00
sd(hu_Intercept)	1.32	0.47	0.50	2.36	1282	1.00

```

Population-Level Effects:

```

	Estimate	Est.Error	l-95% CI	u-95% CI	Eff.Sample	Rhat
Intercept	-6.15	1.95	-10.06	-2.19	3778	1.00
hu_Intercept	2.27	3.33	-3.52	9.67	2755	1.00
bill	0.03	0.02	-0.00	0.07	3480	1.00
pace.tot	-0.41	0.25	-0.90	0.09	4931	1.00
ttlt	-0.00	0.00	-0.01	-0.00	3960	1.00
altTRUE	0.05	0.54	-1.02	1.12	3965	1.00
prop.sew	-1.17	0.98	-3.04	0.77	5212	1.00
ttlt:altTRUE	0.01	0.00	-0.00	0.01	3729	1.00
hu_bill	-0.02	0.03	-0.09	0.03	2784	1.00
hu_pace.tot	0.50	0.36	-0.18	1.24	5686	1.00
hu_ttlt	-0.00	0.00	-0.01	0.01	4466	1.00
hu_altTRUE	0.50	0.85	-1.13	2.17	3961	1.00
hu_prop.sew	3.79	1.57	1.03	7.31	3760	1.00
hu_ttlt:altTRUE	-0.00	0.01	-0.01	0.01	3887	1.00

```

Family Specific Parameters:

```

	Estimate	Est.Error	l-95% CI	u-95% CI	Eff.Sample	Rhat
sigma	0.74	0.12	0.54	1.01	1613	1.00

Samples were drawn using sampling(NUTS). For each parameter, Eff.Sample is a crude measure of effective sample size, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

Figure 7: Log-normal hurdle model of worm intake rates.

The model outputs included next (Figures 8-14) are only those selected and summarized in Chapter 3.

Variables:

since.arrival: number of days since a bird first arrived from migration.

hu_: Prefix denoting the hurdle estimates of the model, as in Chapter 2.

```
> summary(timepot)
Family: hurdle_lognormal
Links: mu = identity; sigma = identity; hu = logit
Formula: rate.su ~ since.arrival + (1 | bird)
         hu ~ since.arrival + (1 | bird)
Data: data (Number of observations: 215)
Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
         total post-warmup samples = 4000

Group-Level Effects:
~bird (Number of levels: 34)
      Estimate Est.Error 1-95% CI u-95% CI Eff.Sample Rhat
sd(Intercept)      1.49      0.22   1.12   1.96       791 1.00
sd(hu_Intercept)    1.61      0.49   0.83   2.73      1176 1.00

Population-Level Effects:
      Estimate Est.Error 1-95% CI u-95% CI Eff.Sample Rhat
Intercept      -5.71      0.30  -6.31  -5.10       707 1.00
hu_Intercept    -1.26      0.45  -2.20  -0.43      2286 1.00
since.arrival     0.02      0.02  -0.02   0.06      6032 1.00
hu_since.arrival -0.06      0.04  -0.15   0.03      4947 1.00

Family Specific Parameters:
      Estimate Est.Error 1-95% CI u-95% CI Eff.Sample Rhat
sigma      0.99      0.06   0.87   1.11      3726 1.00

Samples were drawn using sampling(NUTS). For each parameter, Eff.Sample
is a crude measure of effective sample size, and Rhat is the potential
scale reduction factor on split chains (at convergence, Rhat = 1).
```

Figure 8: Log-normal hurdle model of *Potamopyrgus* intake rates over time since arrival.

```

> summary(timeworm)
Family: hurdle_lognormal
Links: mu = identity; sigma = identity; hu = logit
Formula: rate.allworm ~ since.arrival + (1 | bird)
         hu ~ since.arrival + (1 | bird)
Data: data (Number of observations: 215)
Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
         total post-warmup samples = 4000

Group-Level Effects:
~bird (Number of levels: 34)
      Estimate Est.Error 1-95% CI u-95% CI Eff.Sample Rhat
sd(Intercept)      0.57    0.18   0.23   0.95    1419 1.00
sd(hu_Intercept)   2.68    0.64   1.67   4.20    1440 1.00

Population-Level Effects:
      Estimate Est.Error 1-95% CI u-95% CI Eff.Sample Rhat
Intercept      -5.00    0.24  -5.48  -4.54    3162 1.00
hu_Intercept     1.61    0.59   0.51   2.81    1703 1.00
since.arrival     0.01    0.02  -0.04   0.05    6238 1.00
hu_since.arrival -0.09    0.05  -0.19   0.00    6580 1.00

Family Specific Parameters:
      Estimate Est.Error 1-95% CI u-95% CI Eff.Sample Rhat
sigma      0.94    0.09   0.78   1.15    2688 1.00

Samples were drawn using sampling(NUTS). For each parameter, Eff.Sample
is a crude measure of effective sample size, and Rhat is the potential
scale reduction factor on split chains (at convergence, Rhat = 1).

```

Figure 9: Log-normal hurdle model of worm intake rates over time since arrival.

```

> summary(timebiv)
Family: hurdle_lognormal
Links: mu = identity; sigma = identity; hu = logit
Formula: rate.biv ~ since.arrival + (1 | bird)
         hu ~ since.arrival + (1 | bird)
Data: data (Number of observations: 215)
Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
         total post-warmup samples = 4000

Group-Level Effects:
~bird (Number of levels: 34)
      Estimate Est.Error l-95% CI u-95% CI Eff.Sample Rhat
sd(Intercept)      0.45    0.25   0.03    1.03     1212 1.00
sd(hu_Intercept)    0.93    0.48   0.11    1.99      868 1.00

Population-Level Effects:
      Estimate Est.Error l-95% CI u-95% CI Eff.Sample Rhat
Intercept      -3.99    0.34   -4.66   -3.30     3946 1.00
hu_Intercept     2.17    0.46    1.37    3.14     2099 1.00
since.arrival    -0.02    0.04   -0.10    0.07     4722 1.00
hu_since.arrival -0.01    0.05   -0.11    0.08     4967 1.00

Family Specific Parameters:
      Estimate Est.Error l-95% CI u-95% CI Eff.Sample Rhat
sigma      0.87    0.15    0.62    1.20     2178 1.00

Samples were drawn using sampling(NUTS). For each parameter, Eff.Sample
is a crude measure of effective sample size, and Rhat is the potential
scale reduction factor on split chains (at convergence, Rhat = 1).

```

Figure 10: Log-normal hurdle model of *Cyclomactra* bivalve intake rates over time since arrival.

```

> summary(timesiph)
Family: hurdle_lognormal
Links: mu = identity; sigma = identity; hu = logit
Formula: rate.siph ~ since.arrival + (1 | bird)
         hu ~ since.arrival + (1 | bird)
Data: data (Number of observations: 215)
Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
         total post-warmup samples = 4000

Group-Level Effects:
~bird (Number of levels: 34)
      Estimate Est.Error 1-95% CI u-95% CI Eff.Sample Rhat
sd(Intercept)      0.31      0.24   0.02   0.92      1448 1.00
sd(hu_Intercept)    2.14      0.80   0.93   4.07      1650 1.00

Population-Level Effects:
      Estimate Est.Error 1-95% CI u-95% CI Eff.Sample Rhat
Intercept      -5.28      0.29  -5.88  -4.72      2918 1.00
hu_Intercept     4.74      1.04   3.06   7.05      2484 1.00
since.arrival     0.01      0.03  -0.04   0.06      4314 1.00
hu_since.arrival -0.13      0.07  -0.28   0.02      6782 1.00

Family Specific Parameters:
      Estimate Est.Error 1-95% CI u-95% CI Eff.Sample Rhat
sigma      0.49      0.12   0.32   0.78      2932 1.00

Samples were drawn using sampling(NUTS). For each parameter, Eff.Sample
is a crude measure of effective sample size, and Rhat is the potential
scale reduction factor on split chains (at convergence, Rhat = 1).

```

Figure 11: Log-normal hurdle model of siphon intake rates over time since arrival.

```

> summary(timecrab)
Family: hurdle_lognormal
Links: mu = identity; sigma = identity; hu = logit
Formula: rate.crab ~ since.arrival + (1 | bird)
         hu ~ since.arrival + (1 | bird)
Data: data (Number of observations: 215)
Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
         total post-warmup samples = 4000

Group-Level Effects:
~bird (Number of levels: 34)
      Estimate Est.Error l-95% CI u-95% CI Eff.Sample Rhat
sd(Intercept)      0.65      0.35    0.03    1.35      640 1.01
sd(hu_Intercept)    0.97      0.49    0.10    2.05      900 1.00

Population-Level Effects:
      Estimate Est.Error l-95% CI u-95% CI Eff.Sample Rhat
Intercept      -2.35      0.43   -3.20   -1.50     2346 1.00
hu_Intercept     2.55      0.51    1.66    3.66     2112 1.00
since.arrival    -0.05      0.06   -0.16    0.07     1736 1.00
hu_since.arrival -0.03      0.06   -0.14    0.08     3891 1.00

Family Specific Parameters:
      Estimate Est.Error l-95% CI u-95% CI Eff.Sample Rhat
sigma      0.78      0.22    0.43    1.26      772 1.01

Samples were drawn using sampling(NUTS). For each parameter, Eff.Sample
is a crude measure of effective sample size, and Rhat is the potential
scale reduction factor on split chains (at convergence, Rhat = 1).

```

Figure 12: Log-normal hurdle model of crab intake rates over time since arrival.

```

> summary(timefloun)
Family: hurdle_lognormal
Links: mu = identity; sigma = identity; hu = logit
Formula: rate.floun ~ since.arrival + (1 | bird)
         hu ~ since.arrival + (1 | bird)
Data: data (Number of observations: 215)
Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
         total post-warmup samples = 4000

Group-Level Effects:
~bird (Number of levels: 34)
      Estimate Est.Error 1-95% CI u-95% CI Eff.Sample Rhat
sd(Intercept)      0.68    0.31   0.09   1.35       740 1.01
sd(hu_Intercept)   1.96    0.56   1.12   3.30      1354 1.00

Population-Level Effects:
      Estimate Est.Error 1-95% CI u-95% CI Eff.Sample Rhat
Intercept      -5.40    0.39  -6.20  -4.67      1962 1.00
hu_Intercept    1.38    0.54   0.37   2.53      2065 1.00
since.arrival    0.12    0.06  -0.01   0.24      3505 1.00
hu_since.arrival  0.17    0.06   0.06   0.29      4437 1.00

Family Specific Parameters:
      Estimate Est.Error 1-95% CI u-95% CI Eff.Sample Rhat
sigma      1.08    0.15   0.83   1.40      1609 1.00

Samples were drawn using sampling(NUTS). For each parameter, Eff.Sample
is a crude measure of effective sample size, and Rhat is the potential
scale reduction factor on split chains (at convergence, Rhat = 1).

```

Figure 13: Log-normal hurdle model of flounder intake rates over time since arrival.

```

> summary(timesnail)
Family: hurdle_lognormal
Links: mu = identity; sigma = identity; hu = logit
Formula: rate.snail ~ since.arrival + (1 | bird)
         hu ~ since.arrival + (1 | bird)
Data: data (Number of observations: 215)
Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
         total post-warmup samples = 4000

Group-Level Effects:
~bird (Number of levels: 34)
      Estimate Est.Error l-95% CI u-95% CI Eff.Sample Rhat
sd(Intercept)      0.52      0.24    0.07    1.01      927 1.00
sd(hu_Intercept)    1.94      0.55    1.08    3.26     1209 1.00

Population-Level Effects:
      Estimate Est.Error l-95% CI u-95% CI Eff.Sample Rhat
Intercept     -4.40      0.34   -5.07   -3.73     3190 1.00
hu_Intercept    3.25      0.65    2.12    4.65     2282 1.00
since.arrival   0.08      0.04    0.01    0.16     4441 1.00
hu_since.arrival -0.17      0.05   -0.28   -0.07     4384 1.00

Family Specific Parameters:
      Estimate Est.Error l-95% CI u-95% CI Eff.Sample Rhat
sigma      0.86      0.12    0.66    1.14     1906 1.00

Samples were drawn using sampling(NUTS). For each parameter, Eff.Sample
is a crude measure of effective sample size, and Rhat is the potential
scale reduction factor on split chains (at convergence, Rhat = 1).

```

Figure 14: Log-normal hurdle model of *Amphibola* snail intake rates over time since arrival.