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**PROTHONOTARY WARBLER NESTLING DIET AND GROWTH IN RESPONSE TO
VARIATION IN AQUATIC AND TERRESTRIAL FOOD AVAILABILITY**

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science
in Environmental Studies at Virginia Commonwealth University

By

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ABSTRACT

PROTHONOTARY WARBLER NESTLING DIET AND GROWTH IN RESPONSE TO VARIATION IN AQUATIC AND TERRESTRIAL FOOD AVAILABILITY

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Food supply has been suggested as the main determinant of reproductive success in birds. Riparian species can take advantage of seasonal pulses of both terrestrial and aquatic prey, though aquatic resources are often overlooked in studies of diet and reproductive ecology. This study investigates the flux of both aquatic (mayfly) and terrestrial (caterpillar) prey resources and nestling diet of the Prothonotary Warbler throughout the breeding season in two eastern Virginia sites. One site had significantly higher aquatic prey (mayfly) availability. Nestling diet was generally reflective of prey availability, and nestlings grew faster at the site with high aquatic prey availability. At the site with low aquatic prey availability, nestling growth rates and condition were positively correlated with the amount of aquatic prey in the diet. Our results provide evidence that aquatic subsidies are an important resource for nestlings, and are crucial to understanding the breeding ecology of riparian species.

Introduction

Availability of food resources is a main determinant of reproductive success in animals (Daan et al. 1989, Tremblay et al. 2003). This is especially true in altricial species such as songbirds that require a high degree of parental care (Brinkhof and Cave 1997). Studies in a variety of birds have shown that food availability affects reproductive parameters including double brooding rate (Nagy and Holmes 2005), and nestlings have faster growth rates and higher daily nest survival in habitats with greater invertebrate biomass (Duguay et al. 2000) and in artificially food-supplemented nests (Simons and Martin 1990, Brinkhof and Cave 1997). Nestling growth rate is an important metric because lower rates and mass at fledging have been linked to lower post-fledging survival (Best 1977). Studies of food availability in songbirds have focused primarily on species with a relatively simple terrestrial diet (e.g., caterpillar specialists) likely due to the logistical challenges of simultaneously sampling multiple prey types. However, aquatic insect subsidies to riparian predators can be significant for species as varied as arthropods, birds, bats, and herpetofauna (Nakano and Murakami 2001, Sabo and Power 2002, Baxter et al. 2005). Studies of how aquatic prey affect fitness measures (i.e. growth and survival) of terrestrial consumers have only been conducted for lizards (Sabo and Power 2002), even though aquatic prey can account for 50-90% of the energy budget for some bird species (Nakano and Murakami 2001). More research is needed to understand the importance of aquatic prey subsidies in riparian habitats.

In addition to absolute food supply, reproductive success can be affected by the timing of breeding with regard to seasonal resource availability (Dias and Blondel 1996, Seki and Takano 1998, Naef-Daenzer et al. 2000, García-Navas and Sanz 2011). Ideally, the energy-demanding nestling stage should coincide with seasonal resource peaks (Rossmanith et al. 2007). This idea

has been extensively studied in two caterpillar specialists, Great and Blue Tits (*Parus major*, *Parus caeruleus*) in Europe where timing of breeding was found to be synchronized with the peak caterpillar abundance, independent of habitat (Van Noordwijk et al. 1995, Dias and Blondel 1996, Seki and Takano 1998, Naef-Daenzer et al. 2000, Tremblay et al. 2003). The developmental cycle of caterpillars is strongly synchronized with the emergence of tree foliage in early spring and peak abundance is influenced by ambient temperature (Rossmanith et al. 2007), creating seasonal peaks during the breeding season. The degree of synchronization between laying date and caterpillar peak positively affects fledgling size and number (Van Noordwijk et al. 1995, Dias and Blondel 1996, Tremblay et al. 2003).

Other species do not show a strong link between the timing of nestling provisioning and seasonal resource peaks, such as Wood Warblers (*Phylloscopus sibilatrix*) (Maziarz and Wesolowski 2010) and Red-eyed Vireos (*Vireo olivaceus*) (Marshall and Cooper 2004) whose young are in the nest after the caterpillar peak. These species provide evidence for the optimal-timing theory suggested by Daan et al. (1989), which postulates that energy requirements for egg formation are equally important. As a result, most young are in the nest after, rather than during, the resource peak (Daan et al. 1989). Relatively few studies have tested these theories by quantifying the timing of avian reproduction relative to the pulse(s) in resources, especially for species with a varied diet such as those that include both aquatic and terrestrial prey. Aquatic prey resources also show temporal peaks in abundance, and riparian species that optimize the timing of breeding to coincide with such pulses are likely at an advantage, but no studies to date have assessed this.

A further, less studied, means by which food resources can affect reproductive success is through spatial heterogeneity of food availability. It is advantageous for birds to choose sites

with the greatest resource availability (Moorman et al. 2012) as spatial variation in prey abundance is likely to influence reproductive success (Lyons 2005). Fluxes of aquatic invertebrate prey into the terrestrial environment vary spatially as a function of river characteristics as well as the surrounding riparian habitat (Baxter et al. 2005). Rates of aquatic insect emergence generally increase with stream size, and annual emerging insect densities and biomass decrease with distance from the river (Mackenzie and Kaster 2004, Baxter et al. 2005). Terrestrial food resources exhibit spatial variability as well, typically thought to depend on foliage density (Marshall and Cooper 2004). However, few studies have examined spatial variation in food availability, and to our knowledge none have done so for a riparian species.

Nestling diet has recently been studied in conjunction with food availability to determine if variation in food resources is mirrored in the prey items parents bring to the nest. Within a season, nestling diet can reflect seasonal prey abundance (Maziarz and Wesolowski 2010). However, studies of nestling diet thus far have focused only on sampling terrestrial resources and have not considered aquatic subsidies that are important to many riparian species (Petit et al. 1990a, Baxter et al. 2005). Therefore, an important step in food availability studies for riparian species is the consideration of both aquatic and terrestrial prey simultaneously and how variation in these sources affects nestling provisioning and growth.

Nestling provisioning and diet dictate the majority of nestling reproductive measures, including growth rate and body condition (Tremblay et al. 2005). Growth rate is the rate at which nestlings develop, and there is often strong selection for rapid growth to fledge as early as possible to avoid predation. However, growth must reach a certain point or nestlings with below average growth can suffer from reduced post fledgling survival (Gebhardt-Henrich and Richner 1998) or longer term effects on fitness, including a decreased ability to obtain a breeding

territory or mate (Richner 1992). Thus, there are benefits for a slower growth rate, including greater physiological development, greater flight ability, and higher fledgling condition (Bosque and Bosque 1995), but the tradeoff of early fledging to avoid predation is a strong selection pressure in favor of faster growth rates for most altricial species. In general, we would expect nestlings in habitats with higher food availability and quality to experience faster growth rates. Body condition (mass adjusted for body size) is another metric for nestling health that has been related to lipid reserves that can buffer against starvation during periods of low food availability, as may be the case as they learn to forage independently, and has been shown to be a good predictor for fledgling survival (Hochachka and Smith 1991). We would therefore expect nestlings in habitats with higher quality and abundant food resources to have higher body condition.

In this study we examined variation in both aquatic and terrestrial food resources of the Prothonotary Warbler (*Protonotaria citrea*), a riparian songbird, and how variation in these resources affects nestling provisioning and diet, and in turn, nestling growth and condition. Specifically we quantified the temporal and spatial variation in caterpillar (Lepidoptera) and mayfly (Ephemeroptera) biomass over the breeding season. These two prey items were observed in previous breeding seasons to be the primary prey items brought to nestlings at one of our study sites. Our second objective was to determine whether variation in terrestrial and aquatic food resources influence Prothonotary nestling provisioning. Specifically, do parents feed resources consistent with their spatial and temporal availability? Lastly, we assessed how diet influences nestling growth rate and body condition as well as overall reproductive success.

Methods

Site and study species

Prothonotary Warblers (*Protonotaria citrea*) are Neotropical migratory birds that nest in bottomland hardwood forests throughout the southeastern United States (Petit 1999). Females lay 4-6 eggs per clutch, and can raise two broods per season, typically one “early” and one “late” clutch (Blem et al. 1999). Their nests are usually in cavities near or over water, and as such, they utilize both aquatic and terrestrial prey resources. Most common prey items include caterpillars and spiders (terrestrial), and mayflies and midges (aquatic subsidies) (Petit et al. 1990a). Preliminary data from nest provisioning videos from the 2013 breeding season show that caterpillars and mayflies are the primary food items fed to nestlings (Bulluck and Dodson, personal obs) and were the prey items on which we focused our sampling efforts. Prothonotary Warblers are cavity nesters and will readily nest in artificial nest boxes, making them an ideal species to study their reproductive ecology and diet.

The specific study population of Prothonotary Warblers has been breeding in nest boxes along the lower James River and its tributaries since 1987 and is subject to an ongoing long-term banding and monitoring project (Blem et al. 1999). This study focused on two established nesting sites: Presquile National Wildlife Refuge (Presquile NWR) and Deep Bottom Park in Henrico County, Virginia (Figure 1). These sites were further classified into backcreek and riverfront sub-sites (Figure 1) because prior observations suggested differences in mayfly abundance in these locations. The distance between sub-sites is approximately 950 m and 930 m at Deep Bottom and Presquile NWR, respectively. Deep Bottom Park is approximately 10 km upstream from Presquile NWR and river width at these sites is 325 m and 185 m, respectively. Both sites are a combination of tidal freshwater swamp and bottomland hardwood forest, with green ash (*Fraxinus pennsylvanica*), red maple (*Acer rubrum*), sycamore (*Platanus occidentalis*), oak (*Quercus* spp.), black gum (*Nyssa sylvatica*), and hornbeam (*Carpinus caroliniana*) as the

dominant tree species. Both sites are situated on river meanders, however the site at Presquile has notably more sedimentation around the oxbow and deposition throughout the creek compared with Deep Bottom. This is likely the result of a channel cut made in 1934 at the base of the oxbow that turned Presquile into a true island.

General Field Methods

Birds

A total of 112 nest boxes were monitored in 2014, 64 boxes at Deep Bottom Park, and 48 boxes at Presquile National Wildlife Refuge. All boxes were checked 2-3 times each week during the breeding season and nest contents recorded to determine nest initiation (date of first egg lay), hatching and completion dates for each clutch. As a double brooding species, there is a natural lull in hatching dates during the season. Therefore, nests with eggs that hatched on 28 May or earlier were classified as first clutch, and nests whose eggs hatched 5 June or later were classified as second clutch. Females were captured at the box during incubation and given a USFWS aluminum band. Wing length, tail length, tarsus length, and mass measurements were recorded for all females. Tarsus length was measured to 0.1mm using dial calipers and mass was measured to 0.1g using a Pesola scale.

Nestlings were given a USFWS aluminum band, and mass and tarsus length of each nestling were measured on two occasions between hatching and fledging (mean age of first weighing was 3-4 days, range 2-8 days, mean age of second weighing was 7-8 days, range 5-10 days, with hatch day=0). Mean growth rates per brood were calculated using the change in mean mass recorded between the first and second weighing dates, divided by the number of days between measurements. Nestling body condition was calculated as the residuals from a

regression of tarsus and mass at second measurement for each age class (days old) separately (Schulte-Hostedde et al. 2005).

Caterpillar Availability

We used branch clipping to estimate caterpillar abundance, using a branch-clipping apparatus and methods described by Johnson (2010). Branch clipping was conducted weekly in 15 m radii plots along near-shore transects in the riverfront and backcreek portions of each site (Figure 1). Each week we collected 3 branch clippings from two randomly selected plots along both riverfront and backcreek (6 riverfront samples and 6 backcreek samples per site) for a total of 24 branch clippings per week between the two sites. Prothonotary Warblers are generalist foliage-gleaning insectivores (Petit et al. 1990b, Johnson 2000) and during the breeding season, both male and female Prothonotary Warblers forage below 6m 90% of the time, concentrating their foraging maneuvers on the middle and outer parts of trees and shrubs (Petit et al. 1990b). We sampled the outer branches of the most common tree species in the plots at heights ranging from 0.5-6m. Within one plot, three branch clippings were taken from three different trees. Tree species and height of sample were recorded.

After a branch was collected and the bag was removed from the pole, it was opened slowly to remove the branch one section at a time. The branch was inspected for invertebrates and all leaves were removed at the petiole and collected. After the branch was removed from the bag, it was thoroughly inspected to ensure any invertebrates that fell into the bag during processing were also collected. Invertebrates were placed in a plastic bag with a cotton ball dampened with 70% isopropyl alcohol. All invertebrates were identified to order. The primary species of caterpillars collected were *Geometridae* spp. Both insects and leaves were dried at 80 °C for at least 24 hours, and dry mass was measured to 0.0001 mg. Caterpillar biomass was

calculated for each branch sample as caterpillar dry mass (mg) divided by leaf dry mass (mg). Weekly averages were calculated by sub site (n = 12 per sub-site) and site (n=12 per site).

Mayfly Availability

We used a combination of Pennsylvania style light traps (Frost 1957) and emergence traps (Davies 1984) to sample mayfly abundance. Emergence traps (0.86 m x 0.86 m) were placed every 50 meters along the riverfront and backcreek transects approximately 10 meters from the shore, totaling four emergence traps per transect, eight per site. Emergence traps were deployed on 28 April and were checked weekly until the first emergence (15 May), after which light traps were used as our primary sampling method. Adult mayflies were collected from the emergence trap using a Heavy Duty Hand Held Aspirator from BioQuip (item number 2820GA). Light traps were set up 30 minutes prior to sunset and samples collected 2 hours after sunset. Minimum temperature during the sampling period, average wind speed, moon phase, and total precipitation were recorded. Collected insects were frozen until processing. Mayflies (Ephemeroptera) were picked from the samples, dried in the oven at 80 °C for at least 24 hours, and dry mass was measured to 0.0001 mg. All mayflies collected were *Hexagenia* spp. Mayfly emergence using emergence traps was quantified as total g dry mass per m² of trap area per week to determine weekly rate of emergence, and as g dry mass m⁻² day⁻¹ since last check to achieve finer resolution. Light trap samples were quantified as total mg of dry mass hour⁻¹ for both site and sub-site.

Nestling Diet

Nestling diet was quantified using video observations. A Canon FS400 hand-held standard-definition camera was placed 2-4m from the nest with a clear view of the nest box for at least 1.09 hours (mean video length was 2.55 hours, range 1.09–3.75 hours). All video

observations were conducted in the mornings (6:00-12:30) when the nestlings were 6-10 days old. A total of 64 nest videos were recorded at Deep Bottom, and 46 at Presquile NWR.

Videos were reviewed for identification of food items brought to the nest. We recorded parent sex, duration of visit, food item ID, and number and size of food item(s) for each visit. Food items were identified to one of the following orders: Lepidoptera (caterpillar - terrestrial), Ephemeroptera (mayfly - aquatic), Araneae (spider - terrestrial), Orthoptera (grasshopper - terrestrial), Odonata (dragonfly - aquatic), Other Terrestrial (Coleoptera and other larvae or pupae) or unknown. In accordance with our sampling efforts, the majority of caterpillars and mayflies observed in video observations were *Geometridae* spp and *Hexagenia* spp, respectively.

The length (size) of food was estimated relative to the parents' bill (1 = smaller than bill, 2 = same size as bill, 3 = larger than bill) following Beck (2010). These size estimations were used to calculate a food score. Food score was calculated for each visit as the food size estimate multiplied by the number of items. These food scores were totaled for each nest. If the item size could not be estimated because the item was too small, it received a size of one.

If an item could not be estimated due to a bad camera angle, fast box approach, or other problem with visualization where the food item was never visualized but the parent was still displaying normal feeding behaviors, it was classified as a non-visualized prey item and did not receive a size score. In these cases, an estimated food score was calculated using the proportions of known items size 1, 2, and 3 for that nest video that were observed. The number of non-visualized prey items was multiplied by each of the size proportions (A). These new values were then multiplied by their corresponding food score size (B). The sum of these values provided an estimated size of the non-visualized unknown item(s) (C). When necessary, this was done for each parent (male and female) separately and added to the total known size food score for a total

adjusted food score for that nest. When an item was not visualized but a parent displayed normal feeding behaviors such as perching on the box entrance and lowering it's head and neck into the box, it was assumed one item was being fed.

(A) (Proportion of known items of size 1) x (# non-visualized items) = # items likely size 1

(Proportion of known items size 2) x (# non-visualized items) = # items likely size 2

(Proportion of known items size 3) x (# non-visualized items) = # items likely size 3

(B) (# of items likely size 1) x (Size 1 food score) = Adjusted size 1 food score for non-visualized items

(# of items likely size 2) x (Size 2 food score) = Adjusted size 2 food score for non-visualized items

(# of items likely size 3) x (Size 3 food score) = Adjusted size 3 food score for non-visualized items

(C) (Adjusted size 1 food score) + (Adjusted size 2 food score) + (Adjusted size 3 food score) = Adjusted foodscore

Food score proportions were calculated for all categories (Lepidoptera, Ephemeroptera, Araneae, Orthoptera, Odonata, Other Terrestrial). Food score proportions were calculated for each nest video as the food score for a particular food type divided by the total known food score. All non-proportion diet variables were standardized by number of nestlings and video length (per chick per hour).

Statistical Analyses

Student's two tailed t-tests were performed to test whether there was spatial variation in insect biomass and for differences in provisioning, diet, and reproductive parameters by site and sub site. Sixteen nests at Deep Bottom were located in the mid-creek, and were excluded from sub-site analyses. A Chi-square test of independence was used to determine if there was a difference in the proportion of double brooding females between sites.

In order to assess the influence of site, date, and weekly availability on the prey types brought to nestlings, we conducted a Multivariate Analysis of Variance (MANOVA) that accounted for the interdependence of different prey types being fed (García-Navas and Sanz 2011). Specifically, the amount of caterpillars brought to a nest is not independent of the amount of mayflies brought to that same nest; the MANOVA tested for changes in prey type simultaneously (overall Wilks' Lambda statistic) as well as for univariate effects on prey types individually. The dependent variables in the MANOVA were total mayfly food score chick⁻¹ hour⁻¹ and total caterpillar food score chick⁻¹ hour⁻¹. The independent variables were site, date and the relative site availability of these prey items the week that the provisioning video was taken (site values for caterpillar and mayfly biomass from branch clippings and light trap samples, respectively). Presquile nests were assigned the weekly mayfly biomass from Deep Bottom for the corresponding week because no mayflies were captured at that site (see results). We also tested for an interaction between site and date on the type of prey delivered to nests.

To determine how diet influences mean nestling growth rate and body condition, we developed linear regression models and used Akaike's Information Criterion (AICc) adjusted for small sample size to compare the models (Burnham and Anderson 2002). Because all provisioning data were collected at the brood level (not for each individual nestling), we used brood mean growth rate and body condition as the response variables in these models. We first assessed predictors that were considered known factors and not the focus of the study (i.e., date, nestling age, brood size and site), and significant predictors were then included in models assessing diet. Due to the co-linearity within diet and provisioning variables, model selection was carried out within these variable types and prior to the formation of global models for each response variable. Table 1 lists all predictors included in the model sets. Age was excluded in the

body condition model as body condition was calculated by age. We tested for co-linearity in the global models using variance inflation factors (VIF). All variables had $VIF < 6$, with most variables having a $VIF < 3$. Each input variable in the global model was standardized as suggested by Gelman (2008) to allow for model averaging. A full submodel set was then created, which resulted in a total model set of 160 and 80 models for growth rate and body condition, respectively. A cut off of $\Delta AICc = 2$ was used to create the model set used to obtain model averaged parameter estimates as suggested by Grueber et al. (2011).

Prior to analyses, weekly mayfly biomass, weekly caterpillar biomass, and food scores were $\log_{10}(x + 1)$ transformed, and all diet proportions were arcsine square root transformed to improve normality. Two nests were parasitized by Brown-headed Cowbirds at Presquile NWR, and were excluded from growth rate and body condition analyses. Seven nests had a brood size of one, three at Presquile NWR and four at Deep Bottom, and were also excluded from growth rate and body condition analyses. Body condition and growth rate models were carried out in R version 3.0.1 (R Core Team 2013) and all other analyses were carried out in JMP 11.2.0 (SAS Institute Inc. 2013). Unless otherwise stated, all means are reported ± 1 standard error.

Results

Spatial variation of prey

Caterpillars were abundant at both sites and there was no variation in weekly caterpillar biomass between sites (mean Deep Bottom caterpillar biomass = 0.45 ± 0.14 , mean Presquile caterpillar biomass = 0.20 ± 0.059 , $t = -1.38$, $df = 20.07$, $p = 0.1832$). There was also no spatial variation in weekly caterpillar biomass between riverfront and backcreek (mean riverfront caterpillar biomass = 0.20 ± 0.059 , mean backcreek caterpillar biomass = 0.38 ± 0.099 , $t = -1.20$, $df = 49.90$, $p = 0.2360$). One mayfly was caught in the vicinity of our nest boxes at Presquile

NWR, in a light trap in the backcreek late in the season (22 June). Therefore, Presquile NWR was not included in the analysis for spatial variation of mayfly biomass. At Deep Bottom, riverfront had greater mayfly biomass than backcreek using light traps (mean riverfront mayfly biomass = 212.8 ± 0.38 , mean backcreek mayfly biomass = 34.5 ± 1.10 , $t = 2.25$, $df = 13.57$, $p = 0.0419$).

Prey availability and bird phenology

At both sites, there were two distinct caterpillar biomass peaks, the largest peak the first week of May and another in mid-July. The day of maximum egg production at both sites (9 May, $n = 113$ nests, 361 eggs) occurred within one week after the peak in caterpillar biomass. The date of maximum nestling demand (19 May, $n = 113$ nests, 214 nestlings) occurred during a time of low caterpillar availability and caterpillar biomass remained relatively low throughout the nestling period (Figure 2). A second, smaller caterpillar peak occurred the week of 14 July after most nestlings had fledged (Figure 2).

At Deep Bottom, mayflies remained abundant throughout the nestling period (Figure 3). The day of maximum egg production and hatch date of the earliest nest (9 May) occurred three days before the first peak in mayfly emergence (12 May). The day of maximum nestling demand occurred during a time of high mayfly biomass, and mayfly biomass stayed high, though somewhat variable, for the duration of the season (Figure 3). A least squares model confirmed that mayfly biomass from the light trap varied as a function of Julian date ($p = 0.0030$) and minimum temperature during sampling period ($p = 0.0135$), explaining 62% of the variation. Rate of mayfly emergence as measured from emergence traps also decreased with date (13 May = $1.55 \text{ mg mayfly biomass m}^{-2} \text{ day}^{-1}$, 18 May = $0.61 \text{ mg mayfly biomass m}^{-2} \text{ day}^{-1}$, 26 May = $0.62 \text{ mg mayfly biomass m}^{-2} \text{ day}^{-1}$, 3 June = $0.54 \text{ mg mayfly biomass m}^{-2} \text{ day}^{-1}$). There was a

two-week difference in mayfly emergence between sub sites (riverfront mayfly emergence = 12 May, backcreek mayfly emergence = 26 May) at Deep Bottom, the only site where mayflies were observed near our boxes. This temporal lag time was not reflected in prey type brought to the nest as there was only a two-day difference in date of first mayfly items fed between the sub sites (riverfront first mayfly items fed = 17 May, backcreek first mayfly items fed = 19 May).

Nestling Diet

Diet video observations were recorded for 110 nests (Deep Bottom $n = 63$, backcreek $n = 18$, riverfront $n = 29$; Presquile $n = 47$, backcreek $n = 23$, riverfront $n = 24$). Data from a total of 2,938 visits were recorded and 72% of prey items were identified out of all ($n = 3,468$) items brought to the nests. There was no difference in the amount of unknown food brought to the nest between sites (Deep Bottom mean unknown food score $\text{chick}^{-1} \text{ hour}^{-1} = 1.24 \pm 0.059$, Presquile mean unknown food score $\text{chick}^{-1} \text{ hour}^{-1} = 1.63 \pm 0.069$, $t = 1.65$, $df = 82.08$, $p = 0.1029$).

Nestling diet differed greatly between sites. More mayflies and aquatic prey were fed to nestlings at Deep Bottom, while more caterpillars and terrestrial prey were fed to nestlings at Presquile (Table 2). Aquatic items (primarily mayflies) comprised 62% of all items brought to nests at Deep Bottom (Figure 4); mayflies, caterpillars (13%), and unknown items (21%) comprised 96% of all prey items. Only rarely did parents bring spiders, grasshoppers, dragonflies and other terrestrial items to nest at Deep Bottom, whereas 55% of items brought to nests at Presquile were terrestrial (Figure 4). These items were primarily caterpillars (32%) and other terrestrial larvae and pupae (14%). Unknown items (40%), spiders (4%), grasshoppers (5%), and dragonflies (2%) made up the rest (Figure 4). Concordant with these proportions, mayflies and caterpillars comprised the largest amount (calculated food score) of identified food in the nestling diet at Deep Bottom, whereas caterpillars and other terrestrial larvae comprised the

largest amount at Presquile (Figure 5). The number of visits (male, female and total) did not differ between sites, though all food score values were higher at Deep Bottom (Table 2). Due to the significant diet differences between sites, we compared sub-sites (riverfront versus backcreek) separately for each site.

At Presquile NWR, greater amounts of mayflies and aquatic prey were brought to boxes located in the backcreek, whereas nestlings in boxes at riverfront were fed greater amounts of caterpillars and terrestrial prey (Table 3). The opposite was observed at Deep Bottom. Nestlings in boxes located on the riverfront at Deep Bottom were fed greater amounts of mayflies and aquatic prey, and there was no difference in the amount of caterpillars brought to nests between riverfront and backcreek (Table 4). In addition, Deep Bottom riverfront nests were generally visited more and provisioned more food from the male parent, and in turn, fed a greater amount of food overall (Table 4).

Nestling Diet and Prey Availability

The MANOVA assessing prey type brought to individual nests demonstrated a significant multivariate effect whereby the amount of mayflies and caterpillars brought to the nests was different (Wilk's Lambda statistic = 0.183, $F_{10, 206} = 27.49$, $p < 0.0001$). Specifically, prey items brought to nestlings differed as a function of weekly mayfly biomass ($F_{2, 103} = 4.48$, $p < 0.0137$), site ($F_{2, 103} = 166.93$, $p < 0.0001$) and date ($F_{2, 103} = 14.04$, $p < 0.0001$) as well as an interaction between site and date ($F_{2, 103} = 9.55$, $p = 0.0002$). The types of prey brought to nestlings did not differ as a function of weekly caterpillar biomass ($F_{2, 103} = 2.47$, $p = 0.0899$), though there was a positive relationship between weekly caterpillar biomass and caterpillar food score. In order to better interpret these MANOVA results, we carried out multiple regressions with one response variable at a time. About 77% of the variation in the amount of mayflies

brought to the nestlings can be explained by weekly mayfly biomass ($p = 0.0248$), site ($p < 0.0001$), date ($p = 0.0002$) and the interaction between site and date ($p = 0.0046$). Significantly more mayflies were fed to nestlings when mayflies were more available at Deep Bottom, the site of higher mayfly availability (Figure 6). Also, significantly more mayflies were fed to nestlings at Deep Bottom than Presquile and this amount declined throughout the season at Deep Bottom but stayed consistently low at Presquile (Figure 7a). About 31% of the variation in caterpillar prey brought to nestlings was explained by weekly mayfly biomass ($p = 0.5227$), site ($p < 0.0001$), date ($p = 0.0019$) and the interaction between site and date ($p = 0.0071$). Significantly more caterpillars were fed to Prothonotary Warbler nestlings at Presquile than Deep Bottom early in the season, but this difference decreased later in the season as more caterpillars were fed to nestlings at Deep Bottom (Figure 7b).

Brood Growth Rate and Body Condition Models

Because of the significant site-level differences in diet (Table 2), we included a site by aquatic food score interaction as a potential predictor of nestling growth rate and body condition. The most supported model for mean growth rate included site, age, brood size, aquatic foodscore, male visits, and the interaction between site and aquatic foodscore ($AICc = 47.29$, $w_i = 0.42$). Model averaged parameter estimates were calculated for all variables included in the best performing models with $\Delta AICc$ values < 2 (Table 5). The parameter estimate confidence intervals for site, brood size, and aquatic foodscore include zero (Table 6), suggesting that they are not strong predictors of mean growth rate, whereas the parameter estimates for age, male visits, and the interaction between site and aquatic foodscore did not include zero. Mean growth rate decreases with nestling age and increases with male visits. At Presquile, nestlings fed a greater amount of aquatic prey had higher growth rates, however the amount of aquatic food had

no effect on nestling growth rate at Deep Bottom (Figure 8). Deep Bottom also had a significantly higher mean growth rate than Presquile (Deep Bottom mean growth rate = 1.28 ± 0.041 , Presquile mean growth rate = 1.13 ± 0.060 , $t = -2.11$, $df = 72.07$, $p = 0.0385$).

Six models predicted mean body condition with $\Delta AICc < 2$ (Table 7). The most supported model for mean body condition included date, brood size, female visits and aquatic foodscore ($AICc = 171.61$, $w_i = 0.26$). Model averaged parameter estimates were calculated for all variables included in the best performing models with $\Delta AICc$ values < 2 (Table 8). The parameter estimates for site, female visits, aquatic foodscore include zero, so there is little evidence that these predictor variables influence mean body condition. However, the parameter estimates for date, brood size, and the interaction between site and aquatic foodscore did not include zero. Specifically, nestling body condition decreased throughout the season and with brood size. At Presquile, nestlings that were fed more aquatic prey had higher body condition, but this was not the case at Deep Bottom (Figure 9). However, there was no difference in body condition between sites (Deep Bottom mean body condition = 0.06 ± 0.066 , Presquile mean body condition = -0.14 ± 0.113 , $t = -1.55$, $df = 65.14$, $p = 0.1241$).

Spatial Variation in Reproductive Success

Although not significant, the difference in body condition sign (positive vs. negative) suggests differences in nestling body condition by site. Due to this and the difference in growth rate, we further examined site differences using a variety of fitness measures (Table 9). Deep Bottom had an earlier mean clutch initiation date (Table 9). There was also a trend of Deep Bottom nests having larger clutch sizes and more double brooding, but these differences were not statistically significant. In addition, nestlings at Presquile remained in the nest longer than nestlings at Deep Bottom (Table 9), which could be related to the slower growth rate observed at

this site.

Discussion

This is the first documentation to our knowledge of aquatic prey subsidies influencing nestling growth and condition in a passerine species. Spatial and temporal variation of aquatic and terrestrial resources was observed in the Prothonotary Warbler nestling diet, and higher brood growth rates were found in the habitat with greater aquatic prey availability. Interestingly, nestling growth rate and condition were positively correlated with the amount of aquatic prey in the diet only at the site with low aquatic prey availability (Presquile), further demonstrating the importance of this resource.

Our site with low aquatic prey availability had lower overall food availability than our site with high aquatic prey availability in regard to both aquatic and terrestrial prey. Though not statistically significant, Presquile had a mean weekly caterpillar biomass almost half that of Deep Bottom. Caterpillars were most available just prior to maximum egg production, suggesting they could be an important energy resource for early season egg laying. This can be discussed in terms of optimal-timing theory, which postulates that energy requirements for egg formation is equally important and, as a result, most young are in the nest after, rather than during, the terrestrial resource peak (Daan et al. 1989). A different trend was observed for aquatic prey. Maximum nestling demand occurred within one week after peak mayfly emergence, and mayflies remained abundant throughout the nestling period of both clutches. As such, it appears that Prothonotary Warblers may time their breeding so that mayfly resources are available during the demanding nestling period.

It is important to note that some of the variation in mayfly biomass observed throughout the season is likely due to sampling error. For example, the minimum temperature was coldest

(15.5 °C) the night of the second light trap sample (18 May), and the majority of mayflies were observed on the ground around the light trap rather than flying into the trap. Thus, the lower mayfly biomass measurement the week after emergence may not be representative of true mayfly availability at that time. Our weekly mayfly biomass measurements are therefore likely a measure of minimum mayfly availability.

In general, Prothonotary Warbler parents fed resources consistent with their overall spatial and temporal availability. Mayflies were fed in relation to their weekly availability (Figure 6), and MANOVA results concluded that caterpillar biomass was a marginally significant predictor of type of prey fed ($p = 0.0899$). Further, weekly caterpillar biomass has a positive linear relationship with caterpillar food score when examined in a univariate manner ($p = 0.0256$). It is also important to note that the site with high prey availability had a seasonal shift in diet to include more caterpillars as mayfly biomass and rate of mayfly emergence decreased (Figure 7). The site with low food availability, however, did not have another prey resource available to shift to as food availability declined throughout the season. Thus, parents at this site consistently fed caterpillars to nestlings throughout the season (Figure 7). The site with lower food availability also had a much more diverse diet suggesting that the Prothonotary Warbler opportunistically feeds on a variety of prey types when necessary. Indeed, other studies have shown that birds switch to alternative prey sources target species (Blondel et al. 1991, García-Navas and Sanz 2011). When mayflies were not as available at Deep Bottom, parents switched to caterpillar resources, and as mayfly resources were not generally available at Presquile, parents had a more diverse diet overall with the resources that were available.

Despite the fact that warblers generally fed prey in relation to their abundance, our data do indicate that mayfly resources may be sought out when in low abundance. Although mayflies

were not found in the vicinity of our nest boxes at Presquile (likely due to sedimentation and lack of suitable burrowing substrate), mayflies were observed being fed to nestlings at this site, though in much lower numbers than at Deep Bottom, suggesting that parents travelled off territory to seek out these resources. Mayflies were observed in large numbers on the west side of the island at Presquile (Dodson and Moy pers. obs.) where there was suitable habitat for *Hexagenia* spp. (pebbly substrate). Mayflies were observed being fed to nestlings at Presquile in 13/43 boxes, most of which were at the backcreek sub-site ($n = 10$) which is closer to the western side of the island (up to 650m) than the riverfront sub-site (>1 km). In the habitat with high aquatic prey availability, parents using backcreek boxes were feeding mayflies before they began to emerge in that microhabitat. These parents had to travel approximately up to 900m to the riverfront to forage for mayflies, which indicates that mayflies are a sought out, high quality prey item. Similar preference has been documented in Blue tits (Tremblay et al. 2005) where in habitats of lower caterpillar availability, parents expanded their foraging radius by a factor of two to forage specifically for caterpillars (the preferred prey item for nestlings).

The amount of aquatic prey in the diet also seems to have implications for nestling growth rate and body condition. In a habitat with low aquatic prey availability, both body condition and growth rate increased with amount of aquatic prey in the nestling diet. These relationships are not seen at our site with higher overall prey availability and aquatic prey availability, likely due to the superabundance of food (Tremblay et al. 2003). Reproductive performance only responds to increases in available food supply up to a certain threshold (Maziarz and Wesolowski 2010), beyond which parameters such as fledgling mass can be independent of food supply (Tremblay et al. 2005). This is known as saturation theory; in the habitat with greater food availability, mayfly abundance may have passed the saturation

threshold (Maziarz and Wesolowski 2010), such that nestling growth and condition were not correlated with the amount of aquatic prey in the diet, though both were higher overall compared to the site with lower food availability. However, at a site under the saturation threshold, the relationship between aquatic prey and reproductive parameters is more apparent; parents who sought out aquatic prey had faster growing, heavier nestlings.

Our results suggest that both nestling body condition and growth rate are influenced by diet. Ideally, parents will feed nestlings food that will promote fast growth to allow for early fledging (to avoid nest predation) at a larger mass (to promote survival post fledging). Based on preferential provisioning, our results indicate that this food type is of aquatic origin. Habitats with higher aquatic prey availability had positive body conditions and higher nestling growth rates. Despite these differences in nestlings, these diet differences between sites does not appear to be affecting overall reproductive success (often measured as the number of young fledged). This may be due to the fact that Presquile nestlings spend more time in the nest, so despite their slow growth rate, they have a longer time period over which to grow and develop. In addition, our nest predation rates are very low (boxes placed on poles over water) reducing the selective pressure for early fledging. This could allow them to leave the nest at equivalent development stages and conditions as nestlings from Deep Bottom. Although the number of young fledged did not significantly differ between habitats, clutch initiation date did. It is well known that food availability decreases throughout the season and that more successful birds breed earlier (Daan et al. 1989, Bulluck et al. 2013). Further, reproductive measures including the number of young fledged and proportion of females to double brood are all higher (though not significantly so) at the site with high aquatic prey availability (Naef-Daenzer et al. 2000, Nagy and Holmes 2005, Bulluck et al. 2013). It thus appears that aquatic prey is an important resource not only for

Prothonotary Warbler nestling growth and condition, but possibly overall reproductive success within a habitat. As this was an observational study, future work is recommended to determine potential differences in nutritional content of caterpillars and mayflies.

Our findings indicate that aquatic resources are important subsidies for a riparian songbird, the Prothonotary Warbler. To our knowledge, this is the first documentation of how aquatic subsidies in the nestling diet influence growth and condition in a passerine species, and adds to our understanding of how aquatic subsidies influence fitness measures in avian systems. Our results suggest that understanding the interdependence between aquatic subsidies and riparian terrestrial consumers is crucial to better understand the breeding ecology of riparian species.

Tables and Figures

Table 1. All provisioning and diet variables considered for growth rate and body condition linear regression models. Each variable was run in a model with the known variables for the corresponding response variable and AICc model selection used to determine the best predictor within the variable type.

Variable Type	Predictor Variables	Description
Known	Age	Age of nestlings at second mass measurement.
	Julian Date	Julian date of second mass measurement.
	Brood Size	Number of nestlings in the box.
	Site	Deep Bottom Park or Presquile NWR.
Provisioning	Male visits	Number of times the male visited the box.
	Female visits	Number of times the female visited the box.
	Total visits	The sum of male and female visits.
	Male foodscore	The total amount of food the male brought to the nest.
	Female foodscore	The total amount of food the female brought to the nest.
	Total foodscore	The sum of male and female foodscore.
Diet	Caterpillar foodscore	The total amount of caterpillars (caterpillar items x associated foodscore) brought to the nest.
	Proportion caterpillar foodscore	The amount of caterpillars (caterpillar foodscore) brought to the box divided by total known foodscore.
	Mayfly foodscore	The total amount of mayflies (mayfly items x associated foodscore) brought to the nest.
	Proportion mayfly foodscore	The amount of mayflies (mayfly foodscore) brought to the box divided by total known foodscore.
	Aquatic foodscore	The amount of aquatic food (mayfly + dragonfly foodscore) brought to the nest during the video observation.
	Proportion aquatic foodscore	The amount of aquatic food (mayfly + dragonfly foodscore) brought to the box divided by total known foodscore.
	Terrestrial foodscore	The amount of terrestrial food (caterpillar + spider + grasshopper + other terrestrial foodscore) brought to the nest.
	Proportion terrestrial foodscore	The amount of terrestrial food (caterpillar + spider + grasshopper + other terrestrial foodscore) brought to the nest divided by total known foodscore.

Table 2. Diet and provisioning differences between sites. Back transformations listed for all transformed foodscore variables. Deep Bottom n = 63, Presquile n = 47. Mean \pm 1 SE reported.

Variable	Deep Bottom	Presquile	<i>p</i> value
Female visits	1.47 \pm 0.104	1.48 \pm 0.107	0.9283
Female foodscore	4.01 \pm 0.086	3.07 \pm 0.059	0.0407
Male visits	1.34 \pm 0.108	1.16 \pm 0.114	0.2604
Male foodscore	3.37 \pm 0.081	2.24 \pm 0.089	0.0109
Total visits	2.81 \pm 0.125	2.65 \pm 0.161	0.4258
Total foodscore	8.33 \pm 0.059	5.61 \pm 0.052	<.0001
Mayfly foodscore	4.89 \pm 0.086	0.41 \pm 0.109	<.0001
Caterpillar foodscore	0.95 \pm 0.061	2.02 \pm 0.067	<.0001
Aquatic foodscore	4.89 \pm 0.083	0.29 \pm 0.050	<.0001
Terrestrial foodscore	1.14 \pm 0.064	3.27 \pm 0.076	<.0001

Table 3. Diet and provisioning differences between sub sites at Presquile National Wildlife Refuge. Back transformations listed for all transformed foodscore variables. Backcreek n = 23, riverfront n = 24. Mean \pm 1 SE reported.

Variable	Backcreek	Riverfront	<i>p</i> value
Female visits	1.41 \pm 0.111	1.55 \pm 0.182	0.5107
Female foodscore	3.07 \pm 0.059	3.07 \pm 0.104	0.9747
Male visits	1.01 \pm 0.145	1.31 \pm 0.174	0.1911
Male foodscore	1.95 \pm 0.119	2.55 \pm 0.130	0.3043
Total visits	2.43 \pm 0.172	2.86 \pm 0.265	0.1706
Total foodscore	5.31 \pm 0.064	6.08 \pm 0.081	0.2665
Mayfly foodscore	0.26 \pm 0.072	0.07 \pm 0.047	0.0583
Caterpillar foodscore	1.63 \pm 0.094	2.55 \pm 0.083	0.0161
Aquatic foodscore	0.41 \pm 0.079	0.15 \pm 0.054	0.0219
Terrestrial foodscore	2.63 \pm 0.107	4.01 \pm 0.104	0.0354

Table 4. Diet differences between sub sites at Deep Bottom. Back transformations listed for all transformed foodscore variables. Backcreek n = 18, riverfront n = 29. Mean \pm 1 SE reported.

Variable	Backcreek	Riverfront	<i>p</i> value
Female visits	1.18 \pm 0.178	1.52 \pm 0.132	0.1388
Female foodscore	3.17 \pm 0.161	4.25 \pm 0.122	0.2656
Male visits	1.09 \pm 0.162	1.43 \pm 0.113	0.0905
Male foodscore	2.63 \pm 0.151	4.37 \pm 0.079	0.0230
Total visits	2.27 \pm 0.263	2.96 \pm 0.153	0.0332
Total foodscore	6.08 \pm 0.151	9.23 \pm 0.064	0.0233
Mayfly foodscore	3.17 \pm 0.216	6.24 \pm 0.089	0.0158
Caterpillar foodscore	0.74 \pm 0.119	0.91 \pm 0.061	0.4517
Aquatic foodscore	3.17 \pm 0.219	6.24 \pm 0.089	0.0167
Terrestrial foodscore	0.86 \pm 0.130	1.09 \pm 0.064	0.3911

Table 5. Top models ($\Delta AICc < 2$) for factors predicting brood growth rate. Columns provide model notation, the number of estimable parameters (K), second order Akaike Information Criterion (AICc), AICc differences compared to the top model ($\Delta AICc$), and the relative likelihood of each model (AICc model weights; w_i).

Model	K	AICc	$\Delta AICc$	w_i
Site + age + brood size + aquatic foodscore + male visits + site*aquatic foodscore	8	47.29	0.00	0.42
Site + age + aquatic foodscore + male visits + site*aquatic foodscore	7	47.69	0.41	0.34
Site + age + brood size + male visits	6	48.47	1.18	0.23

Table 6. Parameter estimates from models predicting brood growth rate. Columns provide model averaged parameter estimates, 95% confidence intervals, and relative importance values.

Parameter	Estimate	Confidence Interval	Relative Importance
Intercept	1.34	(1.191, 1.492)	
Site	0.02	(-0.291, 0.324)	1
Age	-0.27	(-0.376, -0.166)	1
Male visits	0.15	(0.042, 0.250)	1
Aquatic foodscore	0.20	(-0.032, 0.439)	0.77
Site*Aquatic foodscore	0.76	(0.234, 1.295)	0.77
Brood size	0.11	(-0.001, 0.206)	0.66

Table 7. Top models ($\Delta AICc < 2$) for factors predicting brood body condition. Columns provide model notation, the number of estimable parameters (K), second order Akaike Information Criterion (AICc), AICc differences compared to the top model ($\Delta AICc$), and the relative likelihood of each model (AICc model weights; w_i).

Model	K	AICc	$\Delta AICc$	w_i
Julian date + brood size + female visits + aquatic foodscore	6	171.61	0.00	0.26
Julian date + brood size + site + aquatic foodscore + female visits + site*aquatic foodscore	8	172.12	0.50	0.20
Julian date + brood size + site + aquatic foodscore + site*aquatic foodscore	7	172.37	0.76	0.17
Julian date + brood size + site + female visits	6	172.60	0.99	0.16
Julian date + brood size + site	5	173.29	1.68	0.11
Julian date + brood size + aquatic foodscore	5	173.39	1.78	0.10

Table 8. Parameter estimates from models predicting brood body condition. Columns provide model averaged parameter estimates, 95% confidence intervals, and relative importance values.

Parameter	Estimate	Confidence Interval	Relative Importance
(Intercept)	0.08	(-0.181, 0.340)	
Julian date	-0.40	(-0.648, -0.146)	1
Brood size	-0.30	(-0.520, -0.068)	1
Aquatic foodscore	0.42	(-0.058, 0.893)	0.73
Site	0.17	(-0.523, 0.865)	0.64
Female visits	-0.21	(-0.412, -0.011)	0.61
Site*Aquatic foodscore	1.30	(0.272, 2.331)	0.37

Table 9. Reproductive differences between sites (Deep Bottom, $n = 62$ nests; Presquile, $n = 47$ nests).

Reproductive Parameter	Site		p value
	Deep Bottom	Presquile	
Clutch initiation date (first clutch only)	118 ± 0.95	123 ± 0.89	<0.0001
Clutch size	4.5 ± 0.13	4.5 ± 0.11	0.8016
Number of young fledged	3.9 ± 0.17	3.6 ± 0.16	0.3101
Days in nest (completion – hatching date)	11.4 ± 0.17	11.9 ± 0.16	0.0474
Proportion females to double brood	0.35	0.26	0.4256

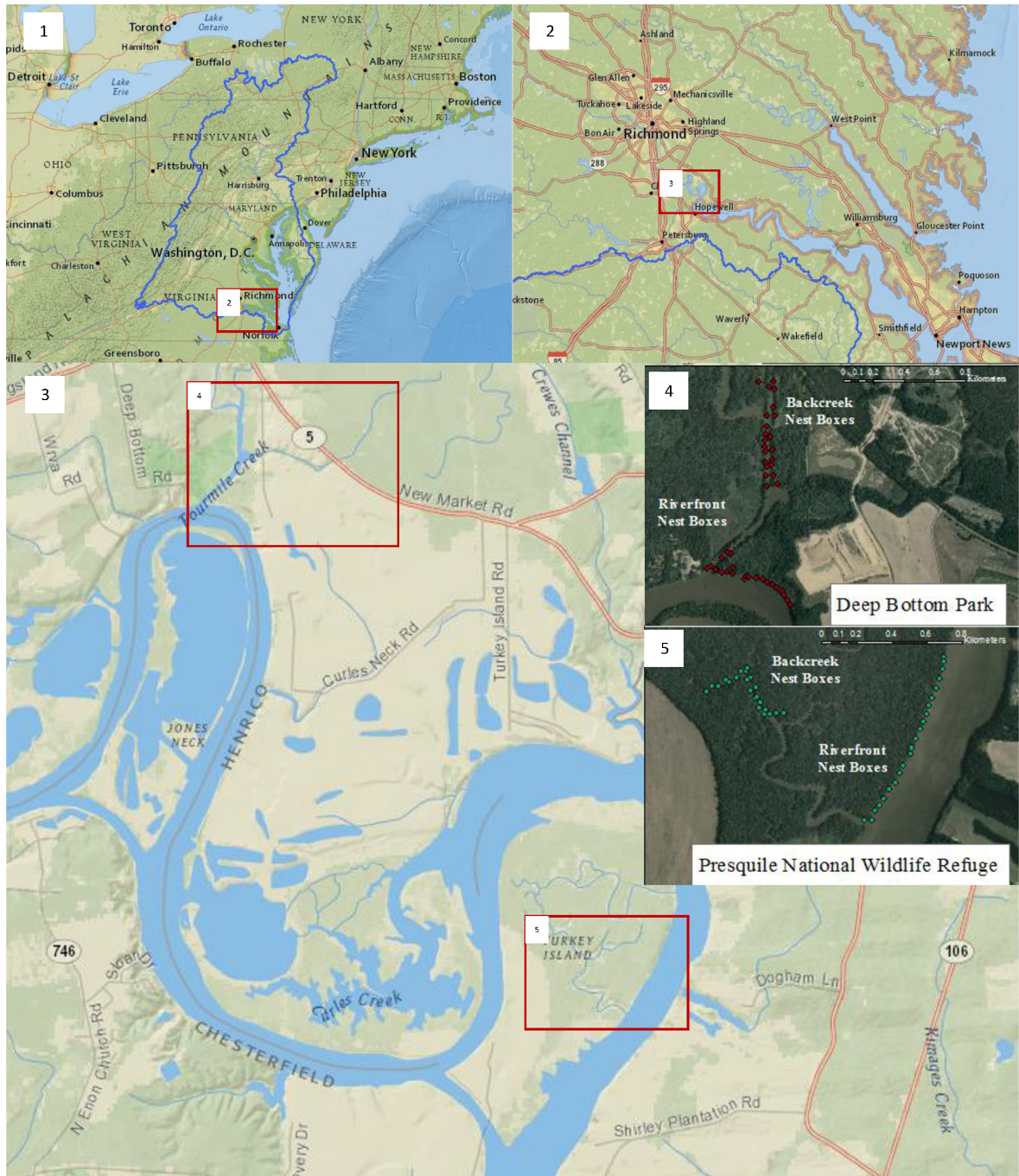


Figure 1. Map of study sites (Deep Bottom Park and Presquile National Wildlife Refuge) and designated sub sites (riverfront and backcreek) located in Henrico County, Virginia. Points in frames 4 and 5 represent nest boxes.

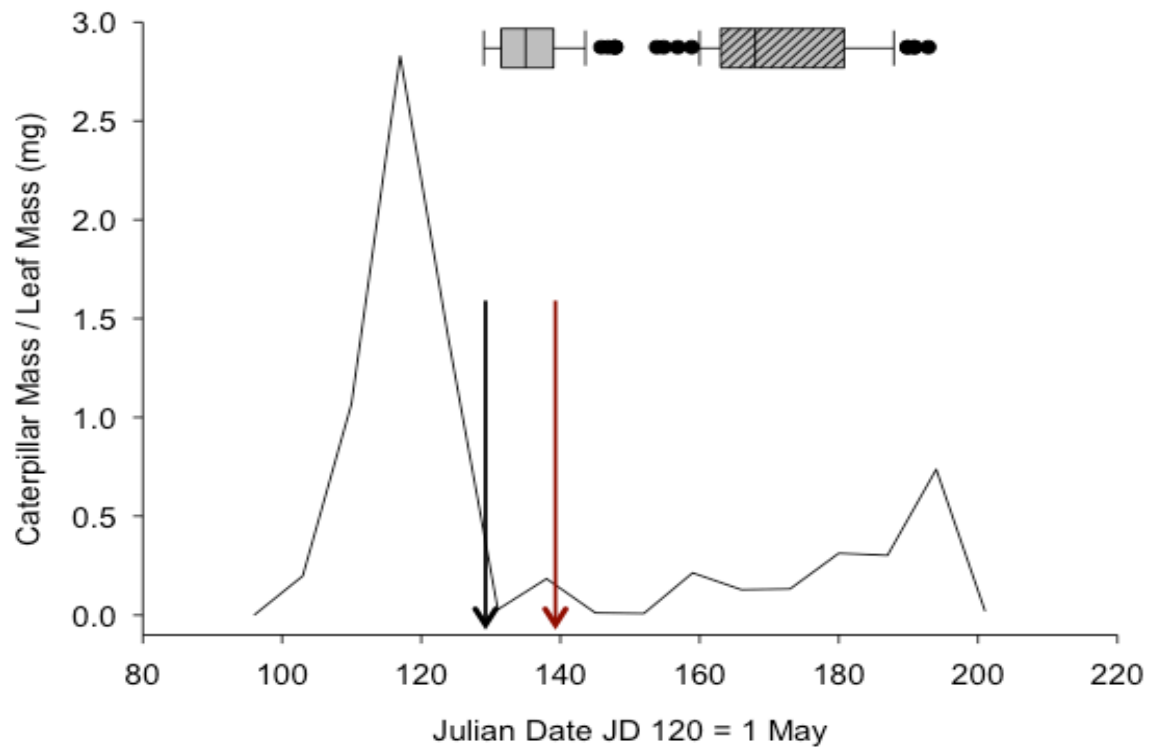


Figure 2. Distribution of Prothonotary Warbler's hatching dates by clutch (box-whiskers; open for first clutch, lined for second clutch) in relation to caterpillar biomass (solid line) at Presquile National Wildlife Refuge and Deep Bottom Park (pooled) throughout the 2014 breeding season. Medians, 25-75% (boxes), minimum-maximum values (whiskers), and outliers (dots) are shown. The black arrow indicates the date of maximum egg production and red arrow indicates the date of maximum nestling demand.

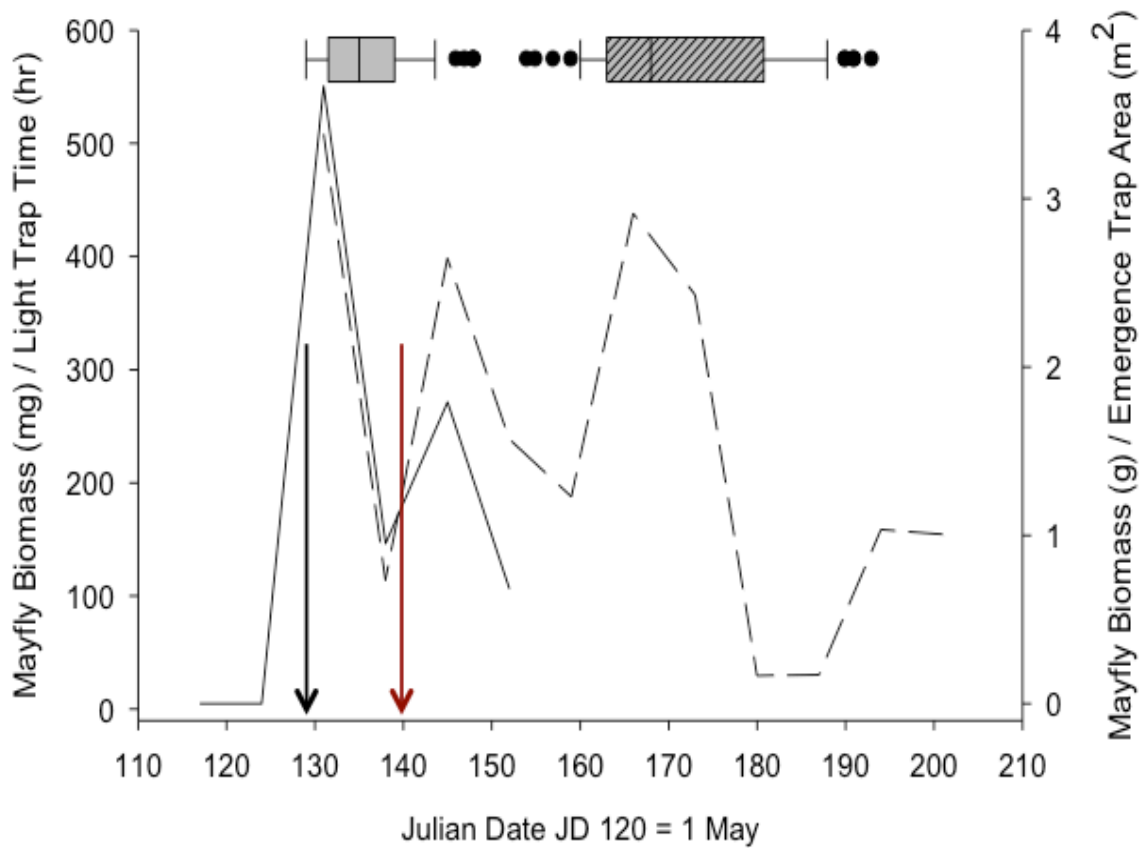


Figure 3. Distribution of Prothonotary Warbler's hatching dates by clutch (box-whiskers; open for first clutch, lined for second clutch) in relation to variation in mayfly biomass from both trap types (solid line emergence traps, dashed line light traps) at Deep Bottom Park throughout the 2014 breeding season. Medians, 25-75% (boxes), minimum-maximum values (whiskers), and outliers (dots) are shown. The black arrow indicates the date of maximum egg production and red arrow indicates the date of maximum nestling demand.

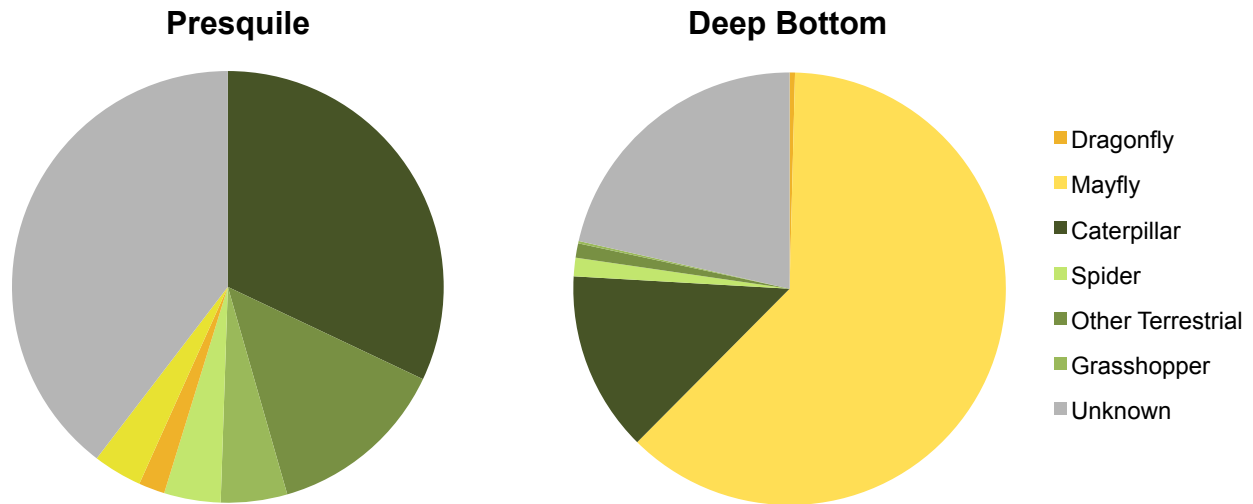


Figure 4. Proportion of prey items in nestling diet by site. Left: Presquile NWR, right: Deep Bottom. Shades of yellow represent aquatic prey items, shades of green represent terrestrial prey items, and gray represents unknown prey items. Parents brought a majority of aquatic prey items at Deep Bottom, particularly mayflies. Parents brought a majority of terrestrial prey items at Presquile with greater diversity to include caterpillar, other terrestrial, grasshopper, and spider items.

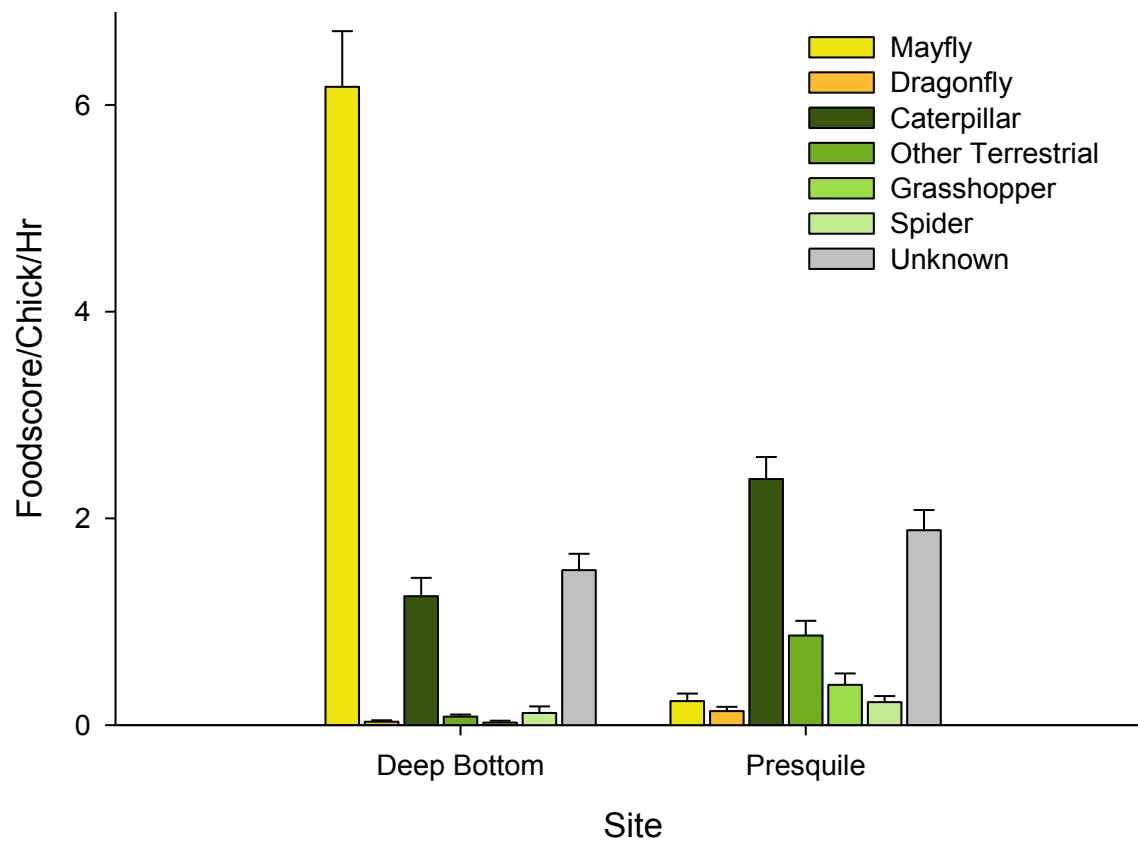


Figure 5. Mean food score of each prey type in nestling diet by site; mean \pm 1 SE. By far, mayflies comprised the greatest amount of identified food in nestling diets at Deep Bottom while caterpillars and other terrestrial comprised the largest amount of identified food in nestling diets at Presquile.

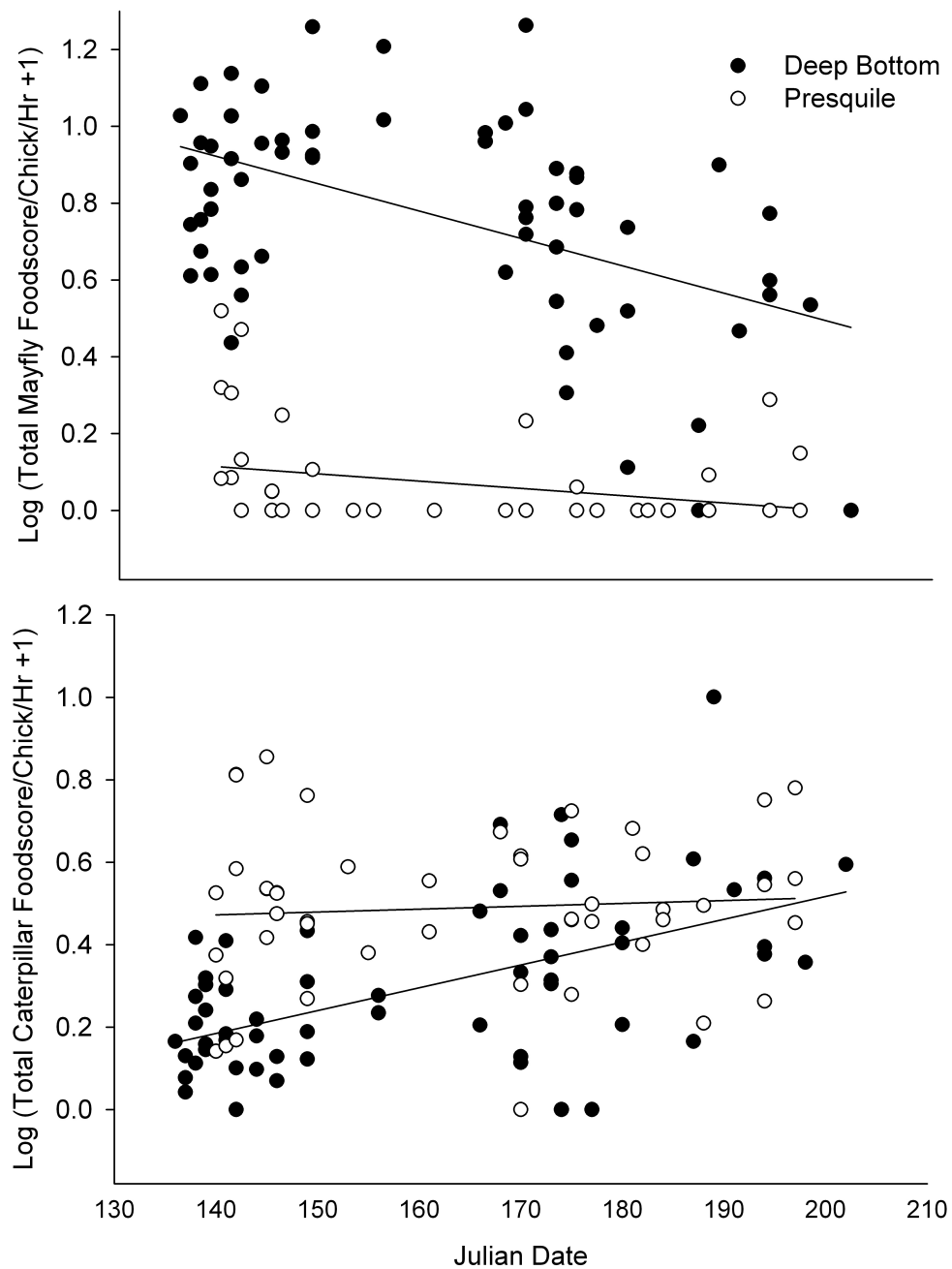


Figure 7. Total mayfly (top) and total caterpillar (bottom) food score as a function of Julian date by site. More mayflies were fed to nestlings at Deep Bottom than Presquile and this amount declined throughout the season at Deep Bottom but stayed consistently low at Presquile. More caterpillars were fed to nestlings at Presquile early in the season, but this difference decreased later in the season as caterpillars began to supplement the decline in mayflies at Deep Bottom.

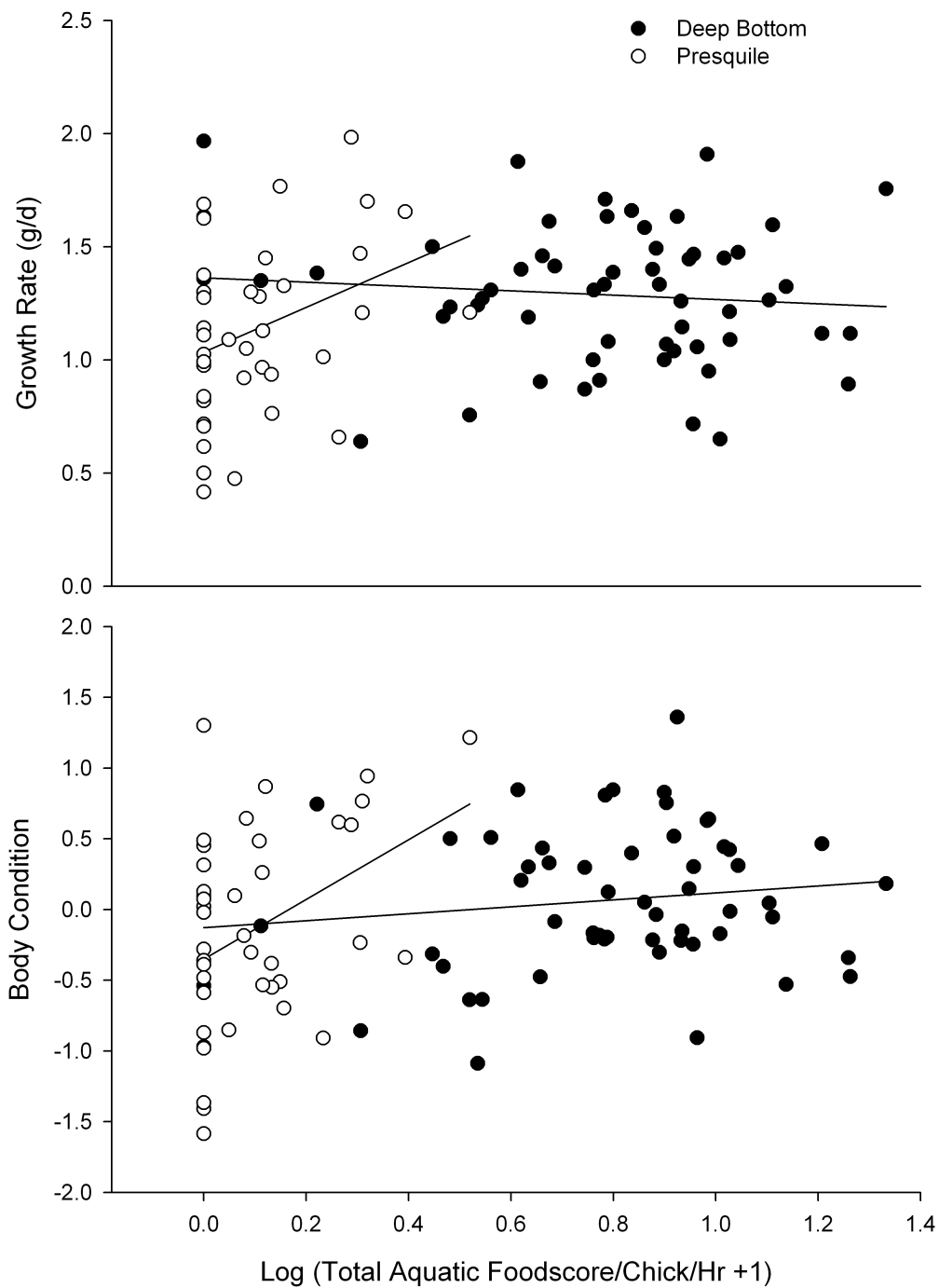


Figure 8. Mean growth rate (top) and mean body condition (bottom) as a function of total aquatic food score by site. At Presquile, nests fed a greater amount of aquatic food had higher growth rates and body conditions. At Deep Bottom, the amount of aquatic food fed had no effect.

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