

Prey Utilization and Energy Demand of a Breeding Peregrine Falcon (*Falco peregrinus*) Population

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## ABSTRACT PAGE

Peregrine Falcons (*Falco peregrinus*) were extirpated from much of their North American breeding range by the mid 1960's, due largely to pesticide poisoning. An intensive recovery effort has restored much of the population to pre-extirpation numbers, although their geographic distribution is now altered from that of the historic population. In the mid-Atlantic, peregrines breed entirely on man-made structures in the coastal plain rather than on naturally-occurring cliff faces in the mountains. This has created conservation conflicts between peregrines and their avian prey. This study was designed to quantify prey usage in Peregrine Falcons, and to estimate their direct impact on prey species of conservation concern. During the 2004 and 2005 breeding seasons prey remains were collected from nest sites on the Virginia portion of the Delmarva peninsula and identified, and this information was combined with images obtained from cameras placed at nests. Prey quantification results showed that this peregrine population is largely dependent on breeding and migrating waterbirds that utilize the area during the Peregrine Falcon breeding season. While no species that are Threatened or Endangered were found to be used as prey, several species of conservation concern were found. Of those, four played a major role in the peregrine diet: Willets (*Tringa semipalmatus*), Short-billed Dowitchers (*Limnodromus griseus*), Ruddy Turnstones (*Arenaria interpres*), and Forster's Terns (*Sterna forsteri*). Using estimates of Field Metabolic Rate based on mass for each bird in the population, energy demand for the total population in 2004 and in 2005 was calculated. These estimates were then used to calculate energy demand for each breeding year since the population recovered. Energy demand estimates were then combined with prey population census data and prey utilization data to estimate the direct impact of breeding peregrines in the coastal plain on species of conservation concern. Ruddy Turnstones are estimated to lose 3.4% of the population (N=1140) to predation from breeding peregrines each year, while Short-billed Dowitchers lose 2.4% (N=2640). Forster's Terns breeding in the vicinity of this peregrine population are estimated to lose 5% (N=247) of the population to predation.

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**Prey Selection of an Artificial Peregrine Falcon Population Breeding on  
Virginia's Eastern Shore**

**ABSTRACT**

After Peregrine Falcons (*Falco peregrinus*) were extirpated from much of their North American breeding range due to widespread use of DDT, restoration efforts relied largely on the release of captive-reared individuals. One area targeted heavily for reintroduction was the coastal plain of the Mid-Atlantic. Peregrines hacked onto man-made structures including towers placed in coastal habitat fared well in part because the area supports a large prey base. In fact, this area is internationally important for many shorebird and waterbird species. Many of the species that depend on this area for migration or breeding and represent potential prey of peregrines are of conservation concern. However, the impact of this expanding breeding population on waterbirds of concern remains unstudied. Here we use prey remains coupled with digital video recording to provide the first documentation of the diet of this peregrine population. We found that peregrines utilized a wide array of species but rely heavily on shorebirds (as much as 52% of the diet). In particular, Willets (*Tringa semipalmatus*), Short-billed Dowitchers (*Limnodromus griseus*), and Ruddy Turnstones (*Arenaria interpres*) are used in large numbers. While many species that are considered to be of conservation concern were found to be used as prey items, no species that are listed as Threatened or Endangered or as Highly Imperiled were used.

## INTRODUCTION

The Peregrine Falcon (*Falco peregrinus*) was listed as endangered in 1970 under the Endangered Species Conservation Act of 1969, a precursor to the Endangered Species Act of 1973. The North American population was extirpated from much of its original range by the mid-1970s mainly due to the use of the pesticide Dichloro-diphenyl-trichloroethane (DDT) which caused eggshell thinning and breeding failure (Berger et al. 1969, Cade *et al.* 1988, Peakall 1976). Due to a ban on DDT and other chlorinated hydrocarbons, successful captive breeding and release, and extensive management, there are now over 2000 pairs of Peregrine Falcons breeding throughout their historic range in the United States (White *et al.* 2002).

While this population recovery includes the breeding population in Virginia, their situation here remains complex. Peregrine Falcons are believed to have been extirpated as a breeding population in Virginia by the mid-1960s (Berger et al. 1969, Cade *et al.* 1988). Historically, Peregrine Falcons in Virginia nested almost exclusively on cliff faces in the mountains of the western part of the state (Hickey 1942, Jones 1946). However, re-introduction of peregrines in Virginia initially focused on the coastal plain region in the hope that an established coastal population, breeding on artificial structures and benefiting from a large food supply and reduced predation from Great-Horned Owls, would eventually serve as a source population for the colonization of the state's western mountains (Hickey 1988). Currently the overwhelming majority of Virginia's breeding peregrine population remains in the vicinity of the initial release area. As of the 2005 breeding season there were 21

occupied breeding territories known for the state; of these, 20 were on man-made structures in the coastal plain and only one was on a cliff in Shenandoah National Park (Watts *et al.* 2005). In effect, the current population of Peregrine Falcons breeding in Virginia is an artificial population existing where none had previously been. While the coastal location does not inherently contain suitable nesting substrate, meaning the falcons must rely on management efforts to maintain nest towers, it does include what is arguably the other most important habitat attribute to breeding raptors, an abundant prey base.

The lower Delmarva Peninsula supports one of the most significant ecosystems along the Atlantic Coast for waterbirds and shorebirds. Its importance as a stronghold for many species of breeding and migrating waterbirds and shorebirds is a large reason for its designation as a Western Hemisphere Shorebird Reserve Network International Site (>100,000 shorebirds/year) (WHSRN 2004), a UNESCO Biosphere Reserve (UNESCO MAB 2008), and an Audubon Important Bird Area (IBA)(Audubon 2004). Large numbers of birds listed as Federal and/or State Threatened or Endangered species, designated for protection in the US Fish and Wildlife Shorebird Conservation Plan (Brown *et al.* 2001) or the North American Waterbird Conservation Plan (Kushlan *et al.* 2002) utilize this area for breeding and migration, and thus become vulnerable to predation by Peregrine Falcons. While this abundance of prey creates excellent habitat for the falcons, it also creates a potential conflict for wildlife managers.

A great deal of effort by a wide range of organizations is put into protecting the habitat and natural resources on the Delmarva (e. g. Wilke *et al.* 2005, Watts and



Truitt 2001) and the Mid-Atlantic coast in general (e.g. Brown *et al.* 2001). In terms of avian species much of that effort is directed toward protection of shorebirds and waterbirds, but a large bit of it also goes toward falcon monitoring and protection. Despite this, there is still little understanding of the interaction between falcons and prey in this avian community, and little information in general on prey selection of this introduced Peregrine Falcon population. To help clarify this issue we undertook a study of Peregrine Falcon prey selection during two consecutive breeding seasons. The objectives of the study were to 1) quantify the prey selection of coastal breeding Peregrine Falcons; 2) determine the importance of shorebirds and waterbirds (particularly those of conservation concern) to the peregrine diet; and 3) understand how prey is used across the population by testing for variation in prey species selection between peregrine pairs.

## **METHODS**

### **Study Area**

All Peregrine Falcon nests used in this study were located in the coastal plain of Virginia. Sites were chosen based on accessibility. One nest was located on a building in the city of Richmond, 4 were on bridges in eastern mainland Virginia, and 13 were located on man-made structures on the Virginia portion of the Delmarva Peninsula (Figure 1, Table 1). Because the main questions of conservation concern involve the Delmarva population, much of the analysis focused on this area.

Flanked to the west by the Chesapeake Bay and to the east by the Atlantic Ocean, the Delmarva Peninsula is roughly 100 kilometers long and varies in width

from under 5 kilometers to approximately 30 kilometers (including the eastern barrier islands). Most of the peninsula is less than 15 meters above sea level and almost uniformly flat. Less than 3% of the total area is structurally developed, while most is wetlands/sand (~44%), with the remainder being cultivated crop or pasture (32%) and forest (total =21%: evergreen =12%, deciduous =8%, and mixed 1%). In 1982 this area was the site of the first successful nesting pair of peregrines in Virginia since the DDT era (VA-07, Figure 1). The population has steadily increased since then but is limited by nest site availability. Since there is no naturally occurring suitable nesting substrate, each nest site is located on an artificial structure. In the majority of cases (n=10), these consist of wooden towers 2-8 meters tall outfitted with a nesting platform, shelter, and gravel, and erected specifically for nesting peregrines. Peregrines also nest successfully here on abandoned fishing shacks, a bridge abutment where nesting substrate has been added, and have also attempted nesting on duck blinds (where they appear to get washed out during high tides). Most are located in salt marshes in the barrier island-lagoon system, are in very close proximity to beach area, and all but one (VA-09, Figure 1) are only a short distance (<5km) from agricultural and/or residential/commercial areas.

Figure 1. Map of nesting locations of Peregrine Falcons in Virginia 2004-2005.

Locations on map correspond to site codes given in Table 1. Sites VA-56, VA-24, VA-22, VA-25, VA-26, and VA-23 are located on the mainland coastal plain, while sites VA-06, VA-09, VA-05, VA-10, VA-18, VA-36, VA-17, VA-62, VA-16, VA-02, VA-34, VA-63, and VA-60 are located on the Virginia portion of the Delmarva Peninsula. All nest sites are on man-made structures.

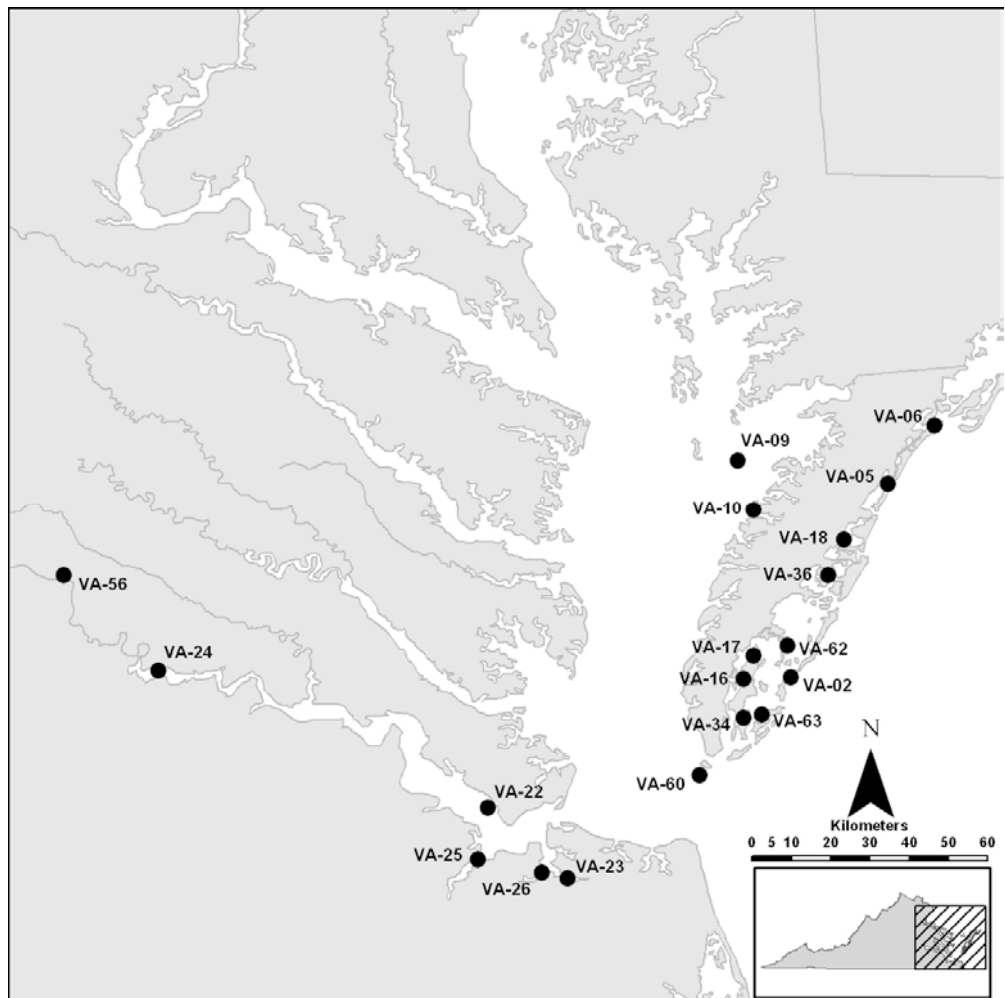


Table 1. Nest codes, locations, and monitoring status for the 2004 and 2005 populations of Peregrine Falcons in Virginia. Nest codes correspond to Figure 1. DVR (Digital Video Recording) and Collections (prey remains collections) indicate sites monitored in the year given using those techniques. Sites listed as NA were not monitored either year using the given technique.

SITE CODE	SITE NAME	DVR	COLLECTIONS
VA-24	Ben Harrison Bridge	2004	2004, 2005
VA-23	Berkeley Bridge	2004	NA
VA-60	Chesapeake Bay Bridge Tunnel	2004	2004
VA-07	Chincoteague	NA	2004
VA-02	Cobb Island	2004	2004
VA-16	Elkins Marsh Chimney	NA	2005
VA-17	Elkins Marsh Shack	2005	2004, 2005
VA-10	Finney's Marsh	2004	2004, 2005
VA-25	Mills Godwin Bridge	NA	2004, 2005
VA-63	Godwin Island	2005	2005
VA-62	Gull Marsh	2005	2005
VA-22	James River Bridge	NA	2004
VA-05	Metomkin Island	2004, 2005	2004, 2005
VA-34	Mockhorn Island	2004, 2005	2004, 2005
VA-36	Upsher Bay tower	2004, 2005	2004, 2005
VA-57	Richmond (BB&T Building)	2004	NA
VA-06	Wallops Island	NA	2005
VA-09	Watts Island	2005	2004, 2005

### Prey Remains Collections and Identification

Prey remains were collected from a total of 16 different nests during the 2004 (n=11) and 2005 (n=15) breeding seasons (Appendix Table 1). Collection dates and

frequency varied from site to site but in general collections were made multiple times throughout the nesting season as early as late April and as late as late July. This time period coincides with the brood-rearing period within the population. Two exceptions were a site that was collected additionally once in November 2004 and a second site that was collected additionally once in October 2005. We chose to include these post-breeding period collection results assuming that they represent prey taken during the breeding season. Because our observations indicate that there is very little activity at the nest sites once the young have dispersed, it is likely that prey present at those times represents breeding-season prey rather than prey utilized only by the adults after the young have left.

Prey remains included feathers, skulls, wings, and legs/feet. During nest visits all prey remains were removed from the nest box and placed in labeled plastic storage bags for later identification. Remains were removed directly from the nest box, from nearby perches, and from the ground below and around the nest. Every attempt was made to remove all remains during each visit. Because peregrines sometimes cache prey for later use, items that appeared to be mostly intact and relatively fresh were noted but left at the site so as not to interfere with provisioning of broods. Pellets were not collected because of the low numbers of pellets present at nests and the difficulties associated with identification of avian prey from falconiform pellets (Marti 1987). Bias toward large species has been shown in studies utilizing only prey remains, so for this reason we assume that the percentage of very small species (*e.g.* warblers, family Parulidae) in the diet may be underrepresented here (Oro and Tella 1995).

Prey remains were identified based on measurements and visual inspection. Wherever possible they were compared against bird specimens housed within the Department of Biology at the College of William and Mary. All identifications were made based on published accounts (Pyle 1997, Prater *et al.* 1977, Hayman *et al.* 1986, Olsen and Larsson 1995, Paulson 2005, Eddleman and Conway 1998, Clark *et al.* 1991). When necessary, experienced ornithologists were consulted for confirmation. Species were identified to the lowest taxonomic group possible. In all but 4 cases remains were identified to the species level.

### **Digital Video Recording and Identification**

In order to supplement information from prey remains collections, Digital Video Recorders (DVRs) were used to record prey items as they were brought to the nest boxes. DVRs were placed at a total of 13 different nests during the 2004 (n=9) and 2005 (n=7) breeding seasons. DVRs from Security Camera World (model SCW-7101) were connected to bullet cameras with 6-mm lens. Systems were powered by marine/RV Deep Cycle batteries and solar panels. Cameras were installed no further than 3 feet from each nest and were aimed to maximize prey images and minimize interference with nesting activities. Cameras were set to record from approximately 05:30 AM through 19:30 PM EDT, although actual recording times varied greatly due to battery life of the unit, available daylight, storage capacity of the compact flash (CF) memory cards, and frequency of nest visits. Depending upon the requirements and possibilities at each site, cameras were set to record images every 10 seconds, 20 seconds, 30 seconds, or were motion-triggered. Images from the DVR were set to

automatically download at the end of each recording day to a 256 MB (CF) card.

Images from CF cards were later downloaded to a Macintosh PowerBook G4.

Camera deployment was timed to achieve the maximum coverage of the post-hatch through pre-fledge stages of nesting that was logistically possible at each site. Camera coverage of nesting stages varied according to accessibility although an attempt was made to cover at least 15 days of post-hatch activity per nest. At some sites coverage started prior to hatching of the first egg, and at some sites coverage continued past banding age (~25-30 days). By this time, though, the chicks are sufficiently mobile and active that they frequently move to areas of the platform adjacent to the nest box. This often means that feeding bouts take place outside of the view of the camera, and therefore coverage past 25 days post-hatch is generally inconsistent.

Prey identification from DVR images was based on visual inspection. When necessary, experienced ornithologists were consulted. Species were identified to the lowest taxonomic group possible, although in many cases no identification was possible due to the view or the condition of the prey item. Despite rapid advancement in the application of photographic equipment in field studies in recent years, there is bias toward species that are easily identified by plumage or other features, although we did not test for this bias. In addition, obtaining appropriate views, equipment failure, and image resolution are known drawbacks to the technique (Marti 1987). However, the use of cameras was preferable to direct observation in this case, as the latter was prohibitive in terms of manpower requirements and access to nests, and would not have resolved any of the above-mentioned issues except equipment failure.

## Analysis

Diet was represented by both the frequency of species and their total biomass. Biomass gives a more accurate representation of a species contribution to diet, while frequency gives a better indication of loss to the prey population. Biomass for each prey species was taken from Dunning (1993). Total biomass for each species was obtained by multiplying the frequency of that species by biomass. Because peregrines frequently cache prey for later use (White *et al.* 2002) it was necessary to categorize items recorded on DVR as new, re-used, or unknown so as not to artificially inflate species tallies. An item was considered new if it had not been seen at the nest previously, or if it was the first item captured on DVR that day. Re-used items were those that had been used at least once previously that day (verified by DVR). If items could not reliably be counted as either new or re-used they were considered to be unknown. When compiling diet from DVR images, only new items were included.

A large number of potential prey species are present in the study area during the migration and breeding seasons. It was necessary to designate these species according to their level of conservation concern. Using categories established by the US Fish and Wildlife Shorebird Conservation Plan (Brown *et al.* 2001) and the North American Waterbird Conservation Plan (Kushlan *et al.* 2002), we selected those present in the study area during the breeding and/or migration seasons given a priority of 3/5 or higher. In order to test for coastal peregrines' dependence on specific groups of prey, items were categorized as breeding shorebirds, migrating shorebirds (shorebirds not generally utilizing the study area for breeding), unknown shorebirds



(where a specific identification could not be made), terns, gulls, rails, ducks, woodpeckers, herons, or passerines (the category “passerines” is used here as a convenient loose grouping of land species not fitting easily into one of the other categories. It is not restricted solely to Passeriformes).

Some individual peregrines have been found to focus predominantly on one prey species or prey group (White *et al.* 2002), therefore not conforming to population norms. These localized effects may be masked in an overall analysis if the other pairs of peregrines do not use these species in large numbers. For this reason we examined the distribution of prey usage across pairs. Because of the conservation concerns associated with peregrine pairs on the Delmarva as opposed to the mainland population, only these (Delmarva) pairs were used when calculating differences in prey species usage across pairs. Pearson’s Chi-squared test with Yate’s correction for continuity were used to evaluate these differences (Sokal and Rohlf 1995). Observed values were the total biomass of that species utilized at each site, while expected values were calculated as that species’ percentage at each site times the total biomass of that species used at all sites. All statistical analysis was done using R (R Development Core Team 2004).

## **RESULTS**

A total of 536 individual prey items were collected during the study. Two hundred and eight items were collected in 2004 and 328 were collected in 2005. We identified 56 species plus 1 unidentified plover species (*Charadrius, spp*), 1 unidentified

sparrow species (*Emberizidae, spp.*), and 2 unidentified warblers (*Parulidae, spp.*).

All prey remains collected were from avian species (App. Table 1).

Over 3000 hours of breeding season nest activity was recorded in 2004 (n=2092) and 2005 (n=982). A total of 1143 separate feeding instances were captured by DVR. Of these, 51% (n=579) were known to be different (new) items, while 11% (n=126) were items that had been used in a previous feeding episode (re-used). The remaining 38% (n=438) could not reliably be categorized as new or re-used (unknown). Of new items, 30% (n=174) were identified to the species level, with 70% (n=405) of items identified to the group level. All identified items were from avian species. Twenty-six species were identified from DVR images, plus 1 unknown plover species (Genus *Charadrius*) and 14 items that were either Common Terns (*Sterna hirundo*) or Forster's Terns (*S. forsteri*) (App. Table 1).

### **Group Frequency and Biomass** (Table 2, Figure 2)

*Shorebirds* Combined shorebird groups (migrating, breeding, and unknown) comprised the highest number and biomass of both prey remains collections (48%, n=255, and 46%, 32.2kg, respectively) and DVR images (52%, n=301, and 61.2%, 31.02kg). These numbers were driven largely by Short-Billed Dowitchers (*Limnodromus griseus*), Willets (*Catoptrophorus semipalmatus*), and Ruddy Turnstones (*Arenaria interpres*).

*Passerines* Of all prey remains collected, passerines comprised the second-highest number of items at 35% (n=187) as well as the second-highest biomass (25%, 17.98kg). They were also the second-highest group of DVR images by number (18.5%, n=107) and biomass (27.4%, 13.87kg). A large number of the items in this

group were Blue Jays (*Cyanocitta cristata*), Common Grackles (*Quiscalus quiscula*), and Crows (American and Fish) (*Corvus brachyrhynchos* and *C. ossifragus*).

*Rails* Rails were the third-most common type of prey remains collected at 7.8% (n=42), as well as the third-highest group by biomass (15%, 10.54kg). They were the fourth-most common group identified through DVR (2.5%, n=11), and third-highest by biomass (6.5%, 3.27kg). The majority were Clapper Rails (*Rallus longirostris*), although several Virginia Rails (*Rallus limicola*) were also taken.

*Terns* Terns were the fourth highest group of prey remains both by number (5.2%, n=28) and biomass (6%, 4.16kg). They were the third most-common group by DVR (2.9%, n=13), and fourth highest by biomass (2.9%, 1.47kg). Most were Common or Forster's Terns, although one Least Tern (*Sterna antillarum*) was also found (Table 5). It should be noted that in the case of the unidentified Common/Forster's Terns, we could not rule out the possibility that they might in fact be Federally Endangered Roseate Terns (*S. dougallii*). In general, however, the nest sites in question were located near known Common or Forster's Tern breeding colonies. In addition, because very few Roseate Terns migrate through the study area and most do so earlier in the season than these items were found, it seems unlikely that any of the items were in fact Roseate Terns.

### **Species Frequency and Biomass**

Rankings of prey items at the species level varied according to whether items were identified by DVR or from prey remains collections, and between frequency and biomass (Table 2, Figure 3). In general, Common Grackles ranked high in all

categories and seem to strongly drive falcon diet in this study area. Other species of note include Willets (highest frequency and biomass of all prey remains collected), Clapper Rails, and Mourning Doves (ranked high for DVR but not for prey remains).

Figure 2. Groupings of avian prey used by Peregrine Falcons during the 2004 and 2005 breeding seasons on the Eastern Shore of Virginia. Graphs reflect prey identified through prey remains collections (Fig. 2A) and Digital Video Recordings (Fig. 2B). Prey species were grouped as Passerines (Pass), Migrating Shorebirds (MISH), Breeding Shorebirds (BRSH), Rails (Rails), Terns (Terns), or Unknown Shorebirds (USH). Values given reflect each group's percentage of the total diet by frequency and biomass.

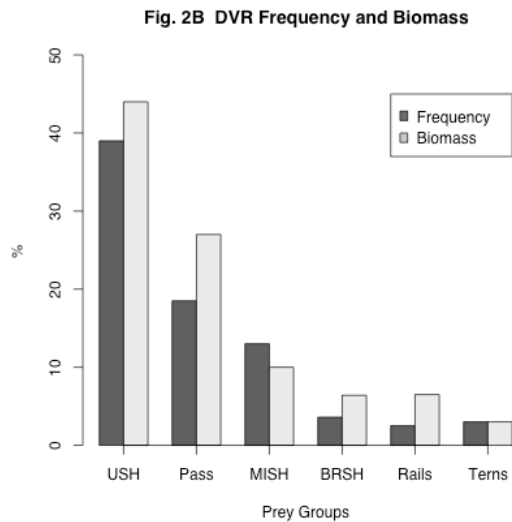
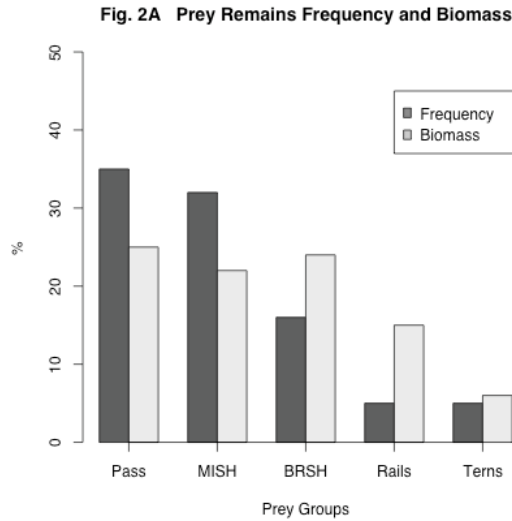
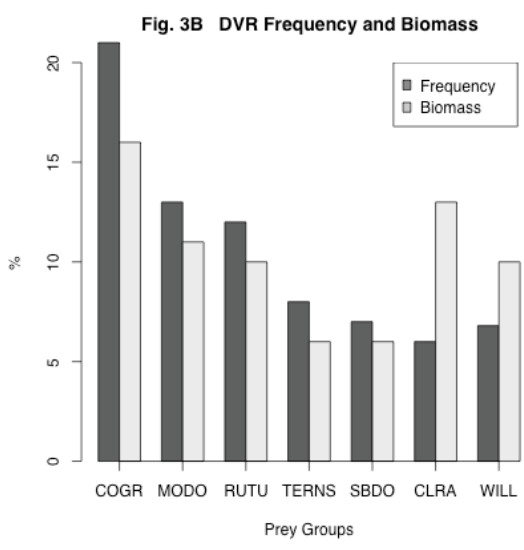
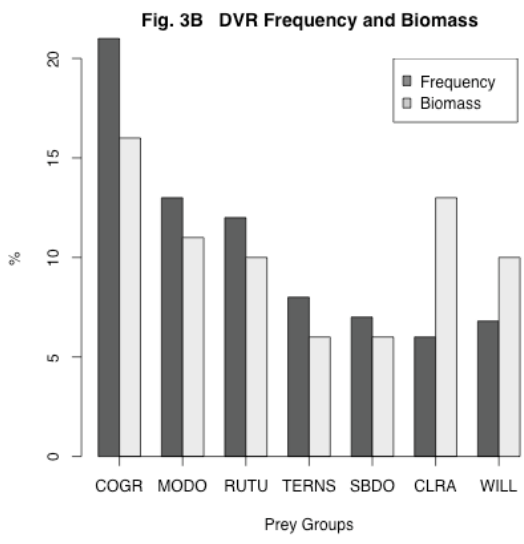


Table 2. Frequency and biomass of different bird groups used as prey by Peregrine Falcons breeding on Virginia's Delmarva Peninsula in 2004 and 2005. Prey refers to prey remains collected from nest sites, while DVR refers to items identified from Digital Video Recorder images recorded at nests. For each group, values are given as both frequency and biomass. Frequency represents the numeric total of each group and its percentage (in parentheses) of the overall total of prey remains collected or DVR items recorded. Individual items were converted to biomass from Dunning (1993) and given as the combined biomass for that group as well as that group's percentage (in parentheses) of the total biomass. The shorebird group was subdivided into migrating shorebirds, breeding shorebirds, and items that could be identified as shorebirds but not identified clearly enough to differentiate between migratory vs. breeding species.

GROUP	PREY FREQUENCY	PREY BIOMASS (kg)	DVR FREQUENCY	DVR BIOMASS (kg)
<i>Shorebirds</i>	255 (48)	32.2 (46)	301 (52)	31 (61)
Migrating	171 (32)	15.6 (22)	58 (13)	5.4 (10.6)
Breeding	84 (16)	16.7 (24)	16 (3.6)	3.2 (6.3)
Unknown	NA	NA	227 (52)	22.4 (44)
<i>Passerines</i>	187 (35)	18 (25)	107 (18.5)	13.9 (27.4)
<i>Rails</i>	42 (7.8)	10.6 (15)	11 (2.5)	3.3 (6.5)
<i>Terns</i>	28 (5.2)	4.2 (6)	13 (2.9)	1.5 (2.9)

Figure 3. Most common prey species used by Peregrine Falcons during the 2004 and 2005 breeding seasons on the Eastern Shore of Virginia. Graphs reflect prey identified through prey remains collections (Fig. 3A) and DVR (Fig. 3B). Prey species included Willets (WILL), Common Grackles (COGR), Short-billed Dowitchers (SBDO), Blue Jays (BLJA), Clapper Rails (CLRA), Mourning Doves (MODO), Ruddy Turnstones (RUTU), and Forster's /Common Terns. (TERNS).



### Species of Conservation Concern

Nine species that were ranked as conservation priority 3 by the US Fish and Wildlife Shorebird Conservation Plan (Brown *et al.* 2001) or the North American Waterbird Conservation Plan (Kushlan *et al.* 2002) were found as prey items:

Killdeer (*Charadrius vociferous*), Greater Yellowlegs (*Tringa melanoleuca*), Lesser Yellowlegs (*Tringa flavipes*), Willet, Sanderling (*Calidris alba*), Least Sandpiper (*Calidris minutilla*), Dunlin (*Calidris alpina*), Forster's Tern, and Black-Crowned Night Heron (*Nycticorax nycticorax*). Seven species ranked as priority 4 were used as prey: American Oystercatcher (*Haematopus palliatus*), Marbled Godwit (*Limosa fedoa*), Ruddy Turnstone, Semipalmated Sandpiper (*Calidris pusilla*), Short-billed Dowitcher, Least Tern, and Little Blue Heron (*Egretta caerulea*) (App. Table 1).

In addition to species listed in either of the above-mentioned conservation plans, several species present in the study area during this period are on the Federal and/or State Threatened and Endangered Species list. None of the species listed as threatened or endangered were found as prey items, although the following three species that are listed as state or federal special concern were found: Forster's Tern, Least Tern, and Little Blue Heron (App. Table 1).

Of all the species of conservation concern that were part of the peregrine diet, four played a major role. Willets ranked highest in frequency and biomass of all prey remains collected and fourth in biomass of all species identified by DVR images. Short-billed Dowitchers were the third highest in frequency and fourth highest in biomass of all prey remains collected. Ruddy Turnstones were the third highest in frequency of all DVR-identified species. Those unidentified terns that are believed to



be either Forster's or Common Terns (while not constituting a single identifiable species, are nonetheless included in this list because of Forster's Tern's status as a species of conservation concern) ranked fourth highest in frequency of DVR-identified items.

### **Pair to Pair Variation**

We tested prey species distribution across sites using Chi-squared analysis of the most commonly taken prey species (Common Grackle, Ruddy Turnstone, Short-billed Dowitcher, Willet, Terns). This analysis showed significant differences (Table 3) in the way prey species were distributed across sites, indicating that prey species are taken in different abundance by different falcons. For example, at site VA-62, Common Grackles comprised 7.4% of prey remains by frequency and 6.3% by biomass. By contrast, at site VA-60, Common Grackles comprised 27.5% of prey remains by frequency and 27.9% by biomass. Forster's Terns were not recorded at all at site VA-60, while at site VA-62 they comprised 22.2% of the prey remains by frequency and 26.3% by biomass.

Table 3. Variation of prey species usage between Peregrine Falcon pairs for selected common prey species. Chi-squared value and degrees of freedom (df) for DVR images (first line) and prey remains (second line).

<b>Species</b>	<b>Chi-Squared Value</b>	<b>df</b>	<b>P-value</b>
Common Grackle	14884165	8	<0.01
	29722360	12	<0.01
Ruddy Turnstone	5827397	8	<0.01
	11135249	12	<0.01
Short-billed Dowitcher	2155025	8	<0.01
	46036229	12	<0.01
Willet	6651242	8	<0.01
	183764768	12	<0.01
Terns	2157965	8	<0.01
	17303767	12	<0.01

## DISCUSSION

A tremendous amount of work has been done on the diet of Peregrine Falcons throughout their range (e.g. White *et al.* 2002 and references therein). Previous studies indicate that peregrine diets vary widely according to habitat (and thus prey availability), but generally consist almost entirely of avian prey (White *et al.* 2002). Our results were consistent with this precept, with 100% of the prey used in this study belonging to the class Aves, as well as with previous findings that peregrines take a large range of species as prey (White *et al.* 2002). White *et al.* (2002) report that peregrines are known to use many hundred species of birds, so it was not surprising to find that the peregrines in this study used over 57 different avian species. Columbids are generally believed to be one of the most important groups, and of the other groups present in the area during the study period, shorebirds, ducks, passerines,

woodpeckers, rails, and procellarids are also frequently taken prey (White *et al.* 2002). While our results were somewhat consistent with these findings, peregrine diets overall generally reflect local habitat (and therefore availability) rather than dependence on particular species (White *et al.* 2002).

Prior to their extirpation from the eastern U.S. there is surprisingly little published data on Peregrine Falcon diet. Perhaps the most comprehensive treatment on eastern peregrines prior to the extirpation is from Hickey (1942), where he mentions only that prey was spread over many species of birds, and was unlikely to be a limiting factor in breeding distribution or density (Hickey 1942). Barclay and Cade (1983) state that reintroduced peregrines have “adopted trophic relations virtually identical” to those of pre-extirpation eastern peregrines, feeding heavily on Blue Jays, “small woodland birds,” feral pigeons, and mourning doves, as well as on shorebirds, ducks, and pigeons in coastal environments. At the 1965 Madison, Wisconsin conference on the decline of Peregrine Falcons, discussion indicated that peregrines in the Hudson Bay and New England area relied heavily on Blue Jays, Northern Flickers (*Colaptes auratus*), and “racing pigeons” but not on Feral Rock Pigeons (Hickey 1969). Re-introduced peregrines in Northern New York and New England (cliff-nesting birds far from coastal areas) also rely heavily on Columbids and Passerines (Corser *et al.* 1999).

Because cliff-nesting peregrines in the western U.S. are often in close proximity to coastal areas with avian assemblages similar to those found in our study area, we expected the diet of modern-day eastern coastal-breeding peregrines to more closely resemble that of western coastal birds than of pre-extirpation eastern

peregrines. In the western U. S. peregrines have been shown to rely heavily on shorebirds, ducks, rails, procellarids, alcids, and podicipedids (White *et al.* 2002, Page and Whitacre 1975, Dekker 1998). In general the composition in our study was similar, although we found two main differences. First, we found no evidence of use of procellarids, alcids, or podicipedids and we found only limited use of ducks; second, prey selection in our study population shows a higher percentage of terns, Common Grackles, Blue Jays, and Mourning Doves.

The absence of alcids and podicipedids is easily explained by the fact that they are seldom present in this area during the peregrine breeding season. Procellarids (shearwaters) and ducks, however, are commonly found here and should therefore be considered as potential prey. There are three realistic explanations for this, none of which is mutually exclusive. First, it may reflect a distribution of duties of breeding peregrine pairs. In general, early in the breeding cycle male peregrines do more hunting than females (White *et al.* 2002). Since females are typically ~30% larger than males, they are correspondingly more able and more likely to take larger prey such as shearwaters and ducks. Only 2 ducks were found in this study, and both were small (the American Black Duck was not yet full-grown) and thus within the size range of prey most easily killed by male peregrines (Table 2). It should be noted, however, that several species that are as large or larger than a typical duck or shearwater (*e.g.* Black-crowned Night Heron, Table 2) were found as prey, so this explanation is unlikely to explain the complete absence of these groups. Another likely possibility is that peregrines in this area restrict the majority (if not all) of their hunting to the barrier island/lagoon system and Delmarva interior and thus do not

encounter shearwaters or to a lesser extent ducks in sufficient numbers for them to be important prey. This may simply reflect the abundance of available prey to be had on land or at the shoreline, *i.e.* prey is available in such profusion that the peregrines never venture very far to obtain it, or it may reflect the third explanation: that some feature of ducks and shearwaters makes them unattractive as prey (*e.g.* evasive flight capabilities, etc.). Since shearwaters and ducks are part of the diet in other localities and at other times of year, the first two explanations seem most likely.

The land use pattern described in the preceding paragraph may also explain the other main difference between eastern and western peregrine populations. The increased usage of birds we grouped loosely as passerines indicates that either 1) the hunting range of the falcons in this study area is not limited to the barrier island/lagoon habitat but instead extends inward into the agricultural, grassland, and developed areas of the peninsula with little or no emphasis on off-shore hunting, or 2) that birds from those areas utilize the barrier island/lagoon habitat frequently enough to become targets for peregrines. The hunting range of a peregrine is quite variable and typically reflects prey density (Ratcliffe 1993), but is generally reported to average ~5km from eyrie (White *et al.* 2002, Enderson and Kirven 1983). Since almost all of the eyries in this study are within 5km of the mainland, it is quite reasonable to assume that hunting expeditions frequently take the peregrines into the mainland of the peninsula. This assumption is supported by the peregrines' use of species seldom associated with the extreme barrier island/lagoon habitat, such as orioles (*Icterus* spp.), tanagers (*Piranga* spp.), and warblers.

The heavy reliance on shorebirds does indicate the importance of the barrier-island-lagoon system as a hunting area. While the usage here of passerines is higher than that reported from similar areas, it does not diminish the fact that the overwhelming majority of species used by peregrines in this study are shorebirds. As reflected in Table 2, shorebirds made up the largest percentage of prey items in each of the four measurements used here. When categories from Table 2 are combined to reflect habitat types, groups associated with the barrier island/lagoon system (shorebirds, rails, and terns) are utilized 1.7-3.1 (by prey remains frequency and dvr frequency, respectively) times more often than those generally associated with forest, grassland, or urban habitats (grouped here as passerines). Given previous reports of peregrine diet (*e.g.* White *et al.* 2002) and the abundance of shorebirds present in the study area at this time (*e.g.* Watts and Truitt 2001), it should not be surprising to find that this peregrine population heavily exploits shorebirds.

The most problematic aspect of this reliance comes from the fact that many of the shorebirds in this area are of conservation concern and are present during breeding and/or migration, two critically important periods of their annual cycles. For example, disturbance from predators has been shown to cause decreased stopover time in migrants (Ydenberg *et al.* 2004), and a decrease in foraging time and efficiency in breeding birds (Quinn 1997). These indirect effects are in addition to the more obvious direct effect of being killed by a predator. While this study was not designed to detect these indirect effects, they are important considerations in determining the overall impact of this predator population. Therefore, the low prevalence of most species of conservation concern in the peregrine diet does not

necessarily indicate that these species are not significantly negatively affected by peregrines.

The four species of conservation concern that do play a large role in peregrine diet are all present in sufficiently large numbers in this area that they would regularly be encountered by peregrines (Watts and Truitt 2001, Watts and Byrd 1998). The only caveat to this statement comes from Short-Billed Dowitchers, which do not breed in this area and have generally completed migration by early June. However, we continued to find Short-Billed Dowitcher remains at peregrine nests well into July, long after most had passed through on southward migration but prior to their return migration northward. Peregrine Falcons are famous for exploiting individual birds that are somehow out of place, whether ill, have irregular plumage, or are disoriented and in a foreign environment (White *et al.* 2002 and references therein). We interpret these dowitcher results as evidence of this latter phenomenon, *i.e.* that stragglers remaining after peak migration were either less fit than those that passed through earlier or were young, inexperienced birds and therefore fell prey to opportunistic peregrines.

One other aspect of Peregrine Falcon behavior which we believe is critical to a full understanding of the predator-prey dynamics of this system involve specialization tendencies by individual birds. Individual peregrines have been well documented to imprint or specialize on just a handful of species, or to take one species out of proportion to its availability (White *et al.* 2002). This behavior could have significant effects on a species of conservation concern that occurs locally near a specialist peregrine, and it can also influence interpretation of the overall population's

diet. It was difficult to test for this behavior given the large number of species that were used as prey in this study. However, a Chi-squared analysis of the five most commonly used species does show that prey species usage is not evenly distributed among peregrine pairs. In addition, looking at the raw data indicates that certain pairs do utilize certain prey species more heavily than do other pairs. One notable example of this comes from Forster's/Common Terns. While Forster's or Common Terns were used as prey at 5 sites, at 3 of those sites they were used in very small numbers (3,2, and 1 individual), with the majority of terns taken as prey at only two sites. In both of these cases Forster's Tern breeding colonies are in close proximity (<0.5km) to the peregrine nest. It is difficult to say whether this is truly a case of specialization by peregrines or merely reflects tern availability, but in either case it is an important consideration for population-wide interpretation of results.

Overall, we found that this coastal peregrine population utilizes a wide variety of avian prey and appears to use both the barrier island/lagoon system as well as the interior of the Delmarva peninsula as hunting grounds. One of the driving factors behind the decision to introduce captive-bred peregrines into coastal habitats in the Mid-Atlantic coast was the great availability of prey (Barclay 1988). It seems evident that the peregrine population has been able to utilize this prey base, particularly in the form of breeding and migrating shorebirds and waterbirds. Though our work does not find a heavy dependence on shorebird/waterbird threatened or endangered species, we do find that several species of lower conservation priority are used heavily. In addition, we cannot rule out the possibility that these species may be indirectly affected by breeding peregrines. Finally, we find a great deal of intra-pair



variation in prey species usage across the peregrine population, indicating that further population-level studies should take this into account.

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## **A Bioenergetic Approach to Interpreting Conservation Conflicts Between Predator and Prey**

### **ABSTRACT**

The conservation needs of sympatric species can sometimes be in direct conflict. In the case of predator and prey, protecting the former can be detrimental to the latter. Anecdotal evidence has suggested that this may be the case for Peregrine Falcons (*Falco peregrinus*) breeding in the coastal plain of the eastern United States. This area is a stronghold for breeding and migrating waterbirds, many of which are of serious conservation concern. Here we attempted to estimate the direct impact of these breeding predators on their prey species. We used a bioenergetic approach to estimate energetic demand of the predator population, then combined it with prey utilization data and prey census data to infer extent to which peregrines directly impacted prey populations. We found that most prey species populations are not likely to be strongly affected by peregrine predation during the peregrine breeding season. However, three species of conservation concern, Willets (*Tringa semipalmatus*), Short-billed Dowitchers (*Limnodromus griseus*), Ruddy Turnstones (*Arenaria interpres*), and Forster's Terns (*Sterna forsteri*) may suffer population losses potentially much larger than 1%.

### **INTRODUCTION**

Addressing the conservation concerns of sensitive species is not always straightforward. This is particularly true when planning conservation resources for multiple sympatric species (Barrows et al. 2005). In these situations conservation

needs of different species can come into conflict (Gumm et al. 2008, Gutierrez et al. 2007, Courchamp et al. 2003), often causing much debate and uncertainty over the appropriate course of action (Minteer, and Collins 2005, Dratch et al. 2004, Roemer et al. 2004). This is amplified when the presence of one species is believed to negatively impact another species, as in the case of predator and prey. Trade-offs between species may result in the control or removal of protected predators in order to preserve prey populations, although decisions on when this action may be appropriate remains controversial (Courchamp et al. 2003, West 2002, Minteer and Collins 2005).

Of critical importance to resolving conservation conflicts between species is an understanding of the strength and impact of inter-species interactions (Minteer and Collins 2005, Soule et al. 2003, Soule et al. 2005). In the case of predator and prey, even a generalist predator can have a negative effect on prey populations. As the number of species involved increases, though, this effect can become difficult to quantify. Such is the case with the Peregrine Falcon (*Falco peregrinus*) population in the mid-Atlantic coastal plain of the U. S. The region is important to dozens of sensitive species that could potentially be used as prey by peregrines, and peregrines have been documented killing prey species of conservation concern (Ch 1). Conservation decisions involving this system are difficult owing to the conservation status of both predator and prey.

Peregrine Falcon (*Falco peregrinus*) populations experienced a sudden and drastic decline throughout much of their range in the years following World War II,

mainly due to the use of the pesticide Dichloro-diphenyl-trichloroethane (DDT) (Berger et al. 1969, Hickey 1988, Peakall 1976). Following a ban on DDT and other chlorinated hydrocarbons, successful captive breeding and release, and extensive management, Peregrine Falcons were removed from the Federal Endangered Species List in 1999 although they are still of conservation concern in portions of their range (White *et al.* 2002). The Peregrine Falcon has state-listed conservation status in the mid-Atlantic, although it is in essence an artificial population: In the mid-Atlantic United States, the majority of the population now resides in the coastal plain, rather than occupying the historic eyries of the Appalachian Mountains.

It is this range shift that has created conflicting conservation strategies. The eastern seaboard of North America hosts large numbers of migrating and breeding shorebirds and waterbirds during the peak of the Peregrine Falcon nesting season, and many of them are of conservation concern (e.g. Watts and Byrd 1998, Watts and Truitt 2001, Brown et al. 2001, Kushlan et al. 2002, Erwin et al. 2007, Williams et al. 2007, Brinker et al. 2007). We have documented previously that the peregrine population is heavily reliant on breeding and migrating shorebirds that are abundant during the peregrine breeding season (Ch. 1), and observations of breeding peregrines harassing or killing other sensitive avian species during the migration and breeding seasons are common. These types of direct and indirect effects have been suggested to impact prey populations (e. g. Thirgood et al. 1999, Ydenberg *et al.* 2004, Paine *et al.* 1990, Quinn 1997). However, these interactions are difficult to quantify, owing to the peregrine's wide hunting range, mobility of both the falcons



and their prey, and terrain in which many of these interactions take place (White and Nelson 1991, Enderson and Craig 1997).

As Peregrine Falcon and their associated energetic demands continue to expand within the mid-Atlantic Coastal Plain, it is increasingly important to understand potential impacts to sensitive prey populations. Here we combined prey utilization data (Ch. 1) with metabolic demand calculations in order to estimate the direct effects of these introduced Peregrine Falcons on their prey species' populations. We have used this bioenergetics approach to 1) estimate energy requirements for each demographic category of falcons 2) estimate energy requirement per pair/brood of falcons and per population, and 3) extrapolate potential impacts of peregrines on their prey species, with emphasis on species of conservation concern.

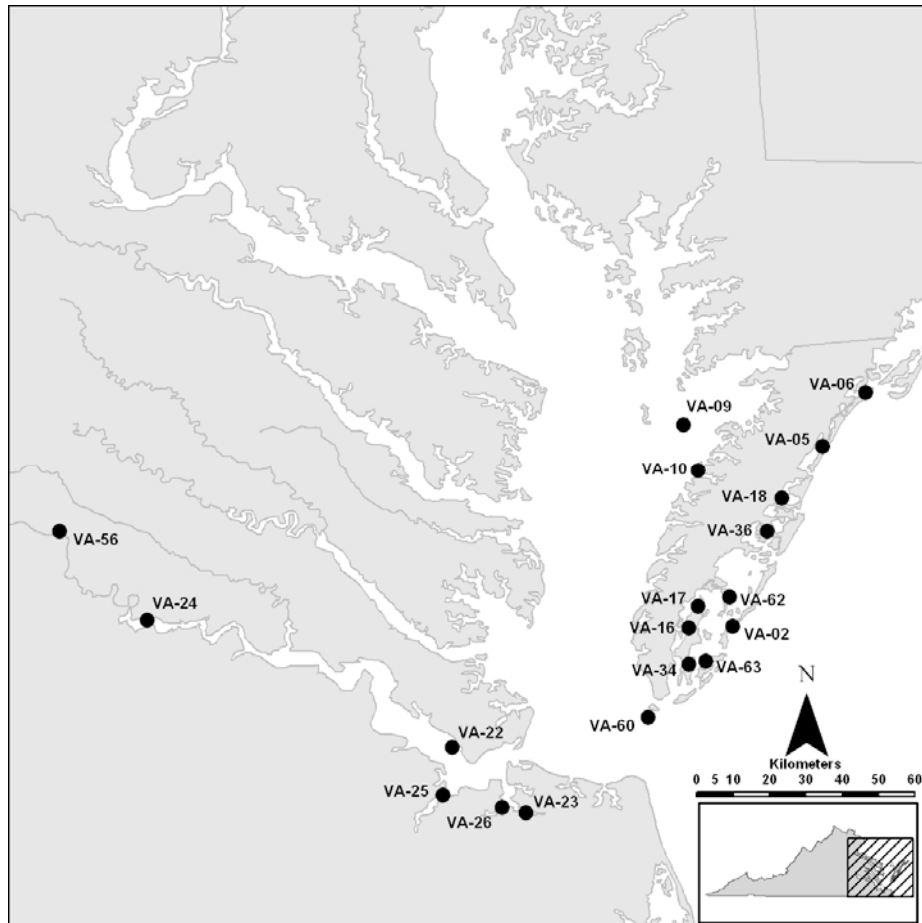
## **METHODS**

### **Study Area**

All nest sites used in this study are located on the Virginia portion of the Delmarva Peninsula (Figure 1, Table 1). Flanked to the west by the Chesapeake Bay and to the east by the Atlantic Ocean, the peninsula is roughly 100 kilometers long and varies in width from under 5 kilometers to approximately 30 kilometers wide (including the eastern barrier islands). Most of the peninsula is less than 15 meters above sea level and almost uniformly flat. Less than 3% of the total area is developed, while most is wetlands/sand (~44%), with the remainder being cultivated

crop and pasture (32%) and forest (total =21%: evergreen =12%, deciduous =8%, and mixed 1%).

**Figure 1.** Map of nesting locations of Peregrine Falcons in Virginia 2004-2005. Locations on map correspond to site codes given in Table 1. Sites VA-56, VA-24, VA-22, VA-25, VA-26, and VA-23 are located on the mainland coastal plain, while sites VA-06, VA-09, VA-05, VA-10, VA-18, VA-36, VA-17, VA-62, VA-16, VA-02, VA-34, VA-63, and VA-60 are located on the Virginia portion of the Delmarva Peninsula. All nest sites are on man-made structures. Only the sites located on the Delmarva were used in this study.



**Table 1.** Nest codes, locations, and monitoring status for the 2004 and 2005 populations of Peregrine Falcons in Virginia. Nest codes correspond to Figure 1. Locations given as Mainland indicate sites west of the Chesapeake Bay, while others are located on the Delmarva Peninsula sea side (eastern peninsula, adjacent to the Atlantic Ocean) or Bay Side (western peninsula, bordering or in the Chesapeake Bay). Only sites located on the Delmarva were used in this study.

SITE CODE	SITE NAME	LOCATION
VA-24	Ben Harrison Bridge	Mainland
VA-23	Berkeley Bridge	Mainland
VA-60	Chesapeake Bay Bridge Tunnel	Delmarva Southern Tip
VA-07	Chincoteague	Delmarva Sea side
VA-02	Cobb Island	Delmarva Sea side
VA-16	Elkins Marsh Chimney	Delmarva Sea side
VA-17	Elkins Marsh Shack	Delmarva Sea side
VA-10	Finney's Marsh	Delmarva Bay side
VA-25	Mills Godwin Bridge	Mainland
VA-63	Godwin Island	Delmarva Sea side
VA-62	Gull Marsh	Delmarva Sea side
VA-22	James River Bridge	Mainland
VA-05	Metomkin Island	Delmarva Sea side
VA-34	Mockhorn Island	Delmarva Sea side
VA-36	Upsher Bay tower	Delmarva Sea side
VA-57	Richmond (BB&T Building)	Mainland
VA-06	Wallops Island	Delmarva Sea side
VA-09	Watts Island	Delmarva Bay side

### Study Population Demography

Peregrines were introduced into the mid-Atlantic coastal plain beginning in 1975 as part of the recovery effort. Using a falconry technique known as hacking,

captive-bred birds were released onto man-made towers and provided with food in the hope that they would establish breeding territories. The first successful nest was recorded in New Jersey in 1979; in the study area (Virginia), releases began in 1977 and the first successful nesting attempt took place on Assateague Island in 1982 (Barclay 1988, Byrd unpublished data). The population has expanded since then, with 13 recorded nesting attempts in 2005 within the study area.

A total of 45 individuals (adults=24, young=21) were present in the 2004 study population, increasing to 53 (adults=26, young=27) in 2005. Of those, all adults are believed to have survived the 2004 season, while 1 adult male is believed to have disappeared or died in the 2005 season. During the 2004 season 17 offspring survived to banding age (25-30 days), and 13 were believed to be alive at the conclusion of the study period. During the 2005 season 25 offspring survived to banding age, and 23 were believed to be alive and present at the conclusion of the study (2 nestlings were removed at one site after the apparent death of the adult male) (Table 2).

**Table 2.** Population Composition of Peregrine Falcon population on the Virginia Portion of the Delmarva Peninsula, 2004 and 2005 breeding seasons. Offspring numbers represent number of hatched young that survived to banding age.

	2004	2005
Number of Adults	24	26
Number of Male offspring	11	18
Number of Female offspring	6	7

### **Energy Requirements**

Peregrine Falcons are known to begin occupying breeding territories in the study area in February and to begin dispersal in early fall. We calculated metabolic demand for each bird in the study population for each day beginning 1 February and ending 30 September for 2004 and 2005, as detailed below. From this metabolic demand, food requirements were then extrapolated. Migratory and overwintering peregrines are known to occupy the study area at times potentially overlapping the study period but are not part of the breeding population and therefore not included in this study. The study period also encompasses the time period of waterbird southward migration, as well as breeding for resident species of waterbirds.

*ADULTS:* Aerial surveys conducted during the 2004 and 2005 breeding seasons identified all occupied territories in the study area (Watts et. al 2004, Watts et. al 2005). For each occupied territory, an energy requirement was calculated for one

male and one female adult. Known departures from these assumptions were factored into the calculations. At non-breeding territories, energy requirements were assumed to remain constant throughout the study period. At breeding territories, energy needs were assumed to remain constant for males but were adjusted for females during laying as described below (Carey 1996).

Field metabolic rate (FMR) was calculated from mass based on Nagy (1987) and Nagy et. al (1999). FMR has not been calculated for peregrines directly and very little data exists on FMR for falconiformes in general, therefore the general formula for all birds was used:

$$FMR(kjoules)/day = 10.5(Mass)^{0.681}$$

This formula may overestimate FMR based on habitat type and time activity budget of peregrines (Nagy 2005, White et. al 2002). However, because activity levels are assumed to rise during this period due to increased hunting in order to provision young, it is likely that metabolic rates are higher during much of this period than at other times of the year, which may balance any over-estimation. Based on published subspecies information (White et. al 2002) and data obtained from asymptotic mass of young in the population (see below), mass of adult males was estimated at 655g and females at 977g.

Once FMR was calculated from mass, an estimate of dietary requirement per day was calculated. Because peregrines prey almost exclusively on birds (in this study there was no evidence of use of non-avian prey), we assumed that all food consumed had an energy density of 6.36 kj/g (Ricklefs 1974). We estimated that

peregrines consume 80% of each prey item, and previous studies indicate they have a digestive efficiency of approximately 75% (White et. al 2002). Therefore, daily food requirements in grams can be calculated using

$$((FMR/6.36)/0.8)/0.75$$

For example, a female Peregrine Falcon with a body mass of 1000g would have a FMR of 1159 kJ/Day and require 304 g/d of avian prey. For reference, Rock Pigeons (*Columba livia*), a common prey item of peregrines, and Willets (*Tringa semipalmatus*), a common prey item in this study, have a biomass of 345.5 g and 215 g, respectively (Dunning 1993).

Female energy requirements were adjusted to account for the cost of egg production by increasing the FMR by 29% during the laying period (FMRI) (Carey 1996):

$$FMRI(kjoules)/day = 1.29 \times (10.5(Mass)^{0.681})$$

In most cases, we were able to determine the onset of laying within 2 days based on nest visits and/or information from Digital Video Recorders (DVRs) placed at the nests. FMR estimations were increased beginning 5 days before the first egg was laid and continued through the final date of laying, after which time the original estimation of FMR was used (White et al. 2002). We did not elevate the estimate of metabolic demand during incubation, as metabolic rates in altricial birds do not change dramatically during this period (Williams 1996)

*YOUNG*: Nests were accessed during the 2004 and 2005 breeding seasons. We attempted to access each nest at least 3 times post-hatching, with the final visit

occurring early enough before fledging to prevent force-fledging but late enough in development to obtain an asymptotic weight (generally between 25 and 30 days post-hatch). In order to obtain a mass estimate for nestlings during the early phase of development when nest visits can be hazardous to chicks, 17 eggs were weighed during the 2005 breeding season and these values were averaged and used for all chicks as mass at day one. This value (41.7g) was similar to published values of egg weights of captive falcons (45.5-47.3 g) (Burnham 1983). In most cases age was determined within 2 days based on our knowledge of hatch dates (see above). When this date could not be positively determined, we estimated age using the formula

$$\text{Age in days} = (\text{Wing length in cm} + 0.84) / 0.69$$

(White et. al 2002). During each nest visit nestlings were weighed using Pesola scales (measured mass,  $M_M$ ) and crop fullness was estimated visually and by palpation on a scale of 0 (completely empty) to 4 (completely full). A full crop can comprise ~10% of total body mass in adult birds (White et. al 2002); therefore to calculate actual body mass ( $M_A$ ), the mass of crop contents ( $M_C$ ) was calculated based on crop score, where a score of 4= 10% of total mass, 3= 7.5%, 2=5%, and 1=2.5%. This value was then subtracted from the measured mass to give actual body mass ( $M_A = M_M - M_C$ ).

Mass for each individual was fitted to a growth curve using the Gompertz equation following Ricklefs (1967). At some sites logistical constraints prohibited sufficient measurements to properly fit a growth curve. In these cases, what data that could be obtained were supplemented by averaging mass across all measured



nestlings and substituting these values for data that were lacking. Because Peregrine Falcons show significant sexual size dimorphism, a separate average was calculated and applied for males versus females. Once a growth curve was calculated for each individual, mass could be estimated for each day in the development phase until asymptotic weight was reached.

Using this mass estimate, FMR was calculated for each nestling for each day of the study period. During the growth period before asymptotic mass was achieved, nestlings were assumed to have an increased FMR equal to twice that of an adult of equal mass (FMR<sub>gr</sub>) (Weathers 1996):

$$FMR_{gr}(kjoules)/day = 2 \times (10.5(Mass)^{0.681})$$

Once asymptote was reached, FMR was calculated as described above for adults.

Calculated values were combined to give the total population energy demand for the study period years, as well as for every year (post-extirpation) that the study area contained breeding or hatched peregrines (1977-2005). A linear regression was calculated for food demand for years 1977-2005 using R (R Development Core Team 2004).

### **Prey Comparisons**

Methods describing prey collection and identification are described in Ch. 1. Briefly, prey identifications were determined by collecting prey remains during nest visits. Prey was identified to the lowest taxonomic order possible. This information was used to determine what proportion of the peregrines' diet was likely

composed of different taxonomic groups, and therefore their direct impact on those populations. For this assessment, the 2004 and 2005 seasons were combined, and prey usage was calculated as a percentage of the total. In addition, we used published studies of migrating shorebirds (Watts and Truitt 2001) and breeding colonial waterbirds (Watts and Byrd 2006) to compare timing of energy demands to abundance of potential prey.

We used population estimates by Morrison et al. (2006) to calculate the percentages of the waterbird populations directly impacted by peregrines. This was done for each species found to comprise >1% of the peregrine diet.

## **RESULTS**

### **Peregrine Demography and Energy Needs**

FMR and energetic demands for each demographic class are shown in Table 3. The population-level analysis estimated that the 2004 population required 2015.9 kilograms of prey during the period studied. Peak energy demand was 13.82 kg of prey and was reached on June 13<sup>th</sup>. The lowest energy demand, 6.3 kg/day, occurred from March 1<sup>st</sup>-March 23 and from April 25<sup>th</sup>-May 5<sup>th</sup> (Figure 2A). The 2005 population required 2508.5 kg of prey, with a peak of 16.88 kg reached on June 1<sup>st</sup>. The minimum requirement, 6.84 kg/day, occurred March 1<sup>st</sup>-March 20<sup>st</sup> and from April 24<sup>th</sup>-April 29<sup>th</sup> (Figure 2B).

Total population food demand was extended to include each year that post-extirpation peregrines were present during the breeding season. Food demand followed an increasing trend (Fig. 3). An  $R^2$  value of 0.86 ( $p < 0.01$ ) was calculated.

**Table 3.** Field metabolic rate (FMR) (kjoule/day) and food requirements (g/day) for each demographic class of breeding Peregrine Falcon, as well as population numbers of each class for the 2004 (n/2004) and 2005 (n/2005) breeding seasons.

	<b>FMR</b>	<b>Food</b>	<b>n/2004</b>	<b>n/2005</b>
<b>Adult Males</b>	866.4	227	12	13
<b>Adult Females (pre/post laying)</b>	1141.1	299	12	13
<b>Adult Females (laying)</b>	1472	386	12	13
<b>Young Male</b>	1712	447	11	18
<b>Young Female</b>	2195	575	6	7

**Figure 2.** Energy requirements of breeding Peregrine Falcons breeding on the Eastern Shore of Virginia, 2004 (Fig. 2A) and 2005 (Fig. 2B). Energy needs were estimated for chicks (dotted line), adults (dashed line), and the total population (solid line) for each day of the season from March 1<sup>st</sup> to Sept. 1<sup>st</sup>. Values given here are times 1000 grams, assuming 75% digestive efficiency of avian prey.

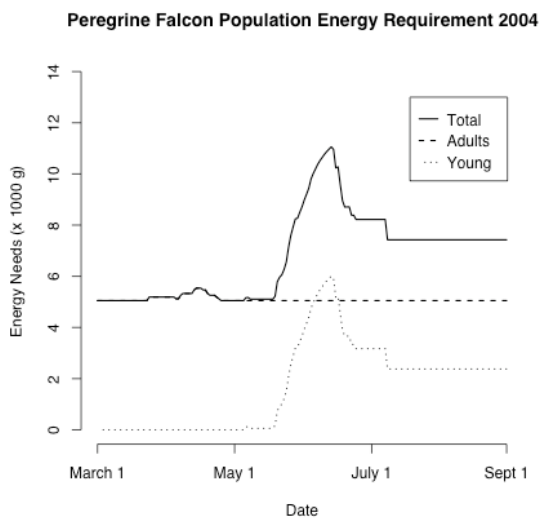


Fig.2A

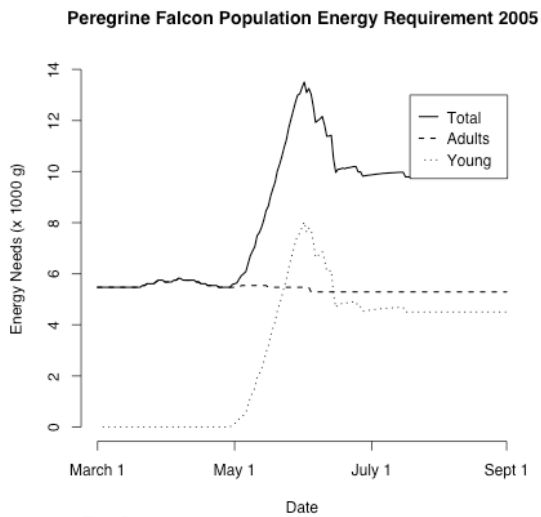


Fig.2B

**Figure 3.** Energy requirement per year for Peregrine Falcon populations breeding on the Virginia Delmarva peninsula. Food demand given in kg.

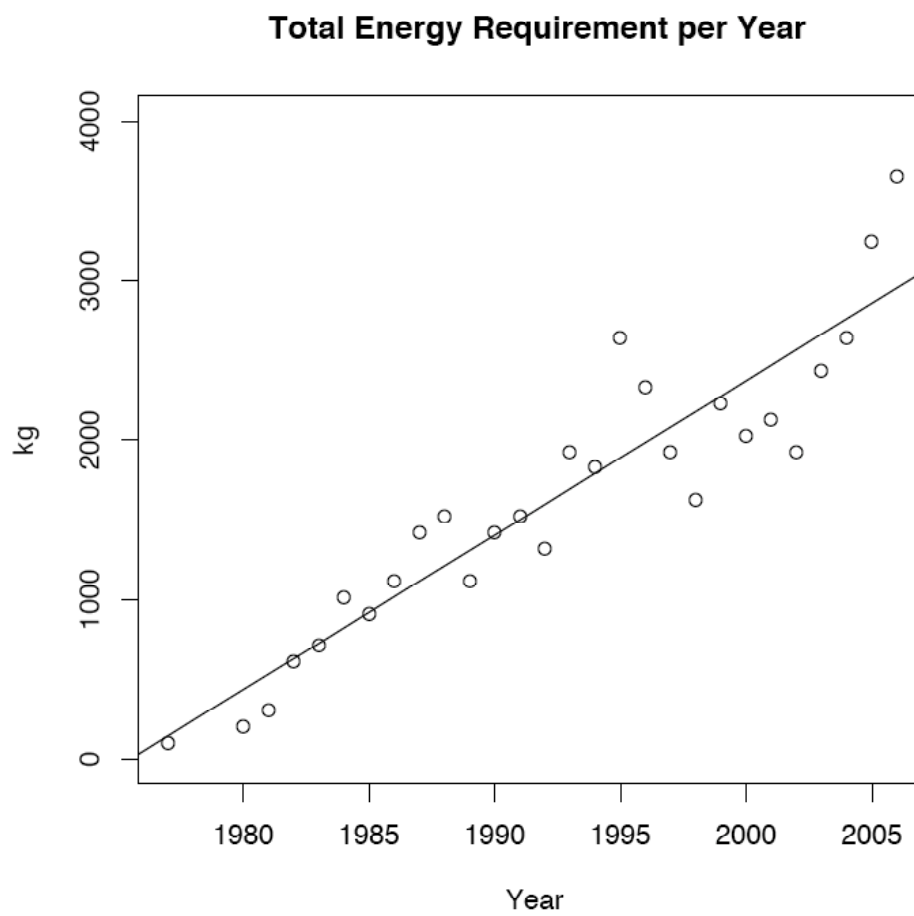


Fig. 3

### **Impact on Prey**

A total of 64.22 kg of prey biomass was recorded in this study, representing <1.5% of the estimated requirement of the falcon population. Biomass of individual prey items ranged from 7.65-883 g, with a median of 113.5 and a mean of 140.2 g.

Published results from migrating shorebird surveys (Watts and Truitt 2001) show that migrating shorebirds in the study area reach their peak around May 21<sup>st</sup>, with 11,893 birds counted in 1995 and 23,170 counted in 1996. During both 2004 and 2005 peregrines had begun hatching by this time, and in the 2005 season this date was 10 days before peak energy demand of the population. Assuming that shorebirds accounted for 61% of the peregrines' diet biomass during this period, peregrines would have required 13.506 kg of food per day at their peak energy requirement and 8.2 kg of that would have been satisfied by shorebirds (~59 individuals per day based on mean biomass of prey items). When converted to biomass, the peak count for shorebirds equates to > 1,707 kg potentially available to the peregrine population (Watts and Truitt 2001, Dunning 1993). The remaining shorebird biomass is 207 times higher than that removed by peregrines. If we assume that during this time peregrines' diet habits change to capitalize on the abundance of shorebirds and they take 100% (~ 96 individuals/day) of their energy needs from this prey group, there is 126 times more shorebird biomass available than the falcon population is likely to consume.

For most prey species, the population loss due to peregrine predation appears to be small (Table 4). However, 3 species were estimated to experience population

losses >1%. Ruddy Turnstones were calculated to lose 3.4% of the population, or 1140 individuals, to peregrine predation, while Short-billed Dowitchers were calculated to lose 2.4% of the population, or 2640 individuals. Forster's Terns were only documented to be used heavily at 2 peregrine nest sites. When the impact of those two sites was calculated separately from the entire peregrine population, it equated to ~5% of the Forster's Tern population breeding in the vicinity, or 247 individuals (Watts and Byrd 2006).

**Table 4.** Estimated direct impacts of breeding Peregrine Falcons on prey populations. Estimates are based on 2005 peregrine energy demand and population estimates by Morrison et al. (2006), except for Laughing Gull population estimates (Watts and Byrd 2006). % pop= estimated percentage of regional prey population taken as prey. N indiv.= estimated number of individuals of regional prey population taken as prey.

<b>Species</b>	<b>% pop</b>	<b>N indiv.</b>
Dunlin	1	2250
Laughing Gull	0.1	118
Lesser Yellowlegs	0.7	1400
Ruddy Turnstone	3.4	1190
Short-billed Dowitcher	2.4	2640
Semi-palmated Sandpiper	0.7	1820

## DISCUSSION

The recovery of the North American Peregrine Falcon has justifiably been heralded as a conservation success story. There is no doubt that a combination of legislation and intensive management has helped to grow the numbers of breeding peregrines throughout much of its North American range, most notably in areas where peregrines were largely or completely extirpated (White *et al.* 2002). As the falcons' numbers increase, though, some prey species populations have dwindled, and in many areas the conservation needs of predator and prey are in conflict. This study was undertaken to help understand the nature and extent of the impact of peregrines on their avian prey populations, and provide a method to estimate these impacts for peregrine populations of varying demographic composition. Generally speaking we found that most prey groups are not drastically reduced by peregrine predation at current population levels. However, the peregrine population is expanding, making it necessary to consider not just the current impact of peregrines on their prey, but the impact of larger future populations as well.

As described above, direct measurements of Peregrine Falcon energy requirements or assessment of impact on prey faces a number of challenges. This type of bioenergetics approach provides a realistic alternative to direct measurement. In cases where the model contains sources of error, we erred on the side of over-estimation of metabolic demand. Even so, the calculations seem to give reasonable estimates of the food requirements of individual birds through different life history



stages. For example, an adult female, non-laying falcon is estimate to require 304 g/day of avian prey, which is only 40g less than a common prey item for peregrines (Rock Pigeon). Once the energy requirements for different demographic categories has been established, the per pair-, per brood-, or per population-demand can be easily estimated as the number of individuals present changes.

The energy estimations calculated here indicate that energy needs fluctuate from year to year, based on the number of breeding pairs in the population and the number, gender, and survivorship of young raised. Although the 2005 population supported just one more breeding pair than the 2004 population, it required almost 309 more kg of food. This difference is not solely attributable to the addition of one breeding pair, as 8 more offspring were produced in 2005 than in 2004. However, a population increase of one pair that produces just one offspring increases the energy requirement by an average of 94.5 kg. Given that the mean biomass of prey was 140.2 g, this would increase the prey take by ~675 individuals, which is sufficiently high to impact certain prey species, particularly if that pair specializes on a particular prey species as peregrines sometimes do.

The prey specialties of individual birds or pairs of birds can potentially have large affects on prey populations. One pair of birds specializing on a prey species with a low population size (e. g. Piping Plovers in this area) could theoretically wipe out or severely diminish that species in as little as one season. Unfortunately this tendency to specialize cannot be predicted, as most peregrines remain generalist avian predators. Although certain life history traits due seem to increase the likelihood of

predation, it is impossible to predict just which species might become the focus of specialist peregrines owing to the breadth of the typical peregrine diet and the diversity of prey present in most areas (White et al. 2002). Only by focused monitoring can the impact of individual pairs be determined. In this case, there was evidence that certain pairs focused on a species (Forster's Tern) but were not true specialists- that is, while one species may have comprised an inordinately high percentage of the diet, the remaining portion of the diet was made up of a wide array of other species. Whether or not the impact of these peregrines on the tern population is drastic would require additional study and demographic modeling. However, it certainly seems possible that the falcons could be having a localized impact on Forster's Tern populations.

One subject that has not been addressed in this study is the proximity of the peregrine territories to their prey populations and the subsequent risk to those prey populations. It would seem likely that prey in close proximity to peregrine nest sites would be at greater predation risk than those at a distance. However, breeding peregrines have been known to hunt as much as 43km from the eyrie, and territory size varies largely between individuals (White and Nelson 1991, Enderson and Craig 1997). It is therefore virtually impossible to determine the territory and/or hunting range of an individual peregrine in this study area and by extension the quantity and composition of the prey available within that territory. Within this peregrine population, hunting ranges between pairs unquestionably overlap, though it is unclear to what extent individuals tolerate one another. Because of this, prey species are

likely to face varying degrees of predation pressure by multiple peregrines, regardless of the peregrines' diet specialties (or lack thereof). Immediate proximity to a falcon nest site does not necessarily increase (or decrease) the likelihood of predation. The example of Forster's Terns given above illustrates this point. While the two peregrine pairs that relied heavily on Forster's Terns are indeed in close proximity to tern colonies (< 1km), five of the other sites in the study are similarly close, and all but one are within 10km of a Forster's Tern colony and thus well-within the hunting range of a typical peregrine (White et al. 2002). Despite this proximity, terns were used only sparsely or not at all at all but the two sites discussed above.

One species that was used heavily by the entire peregrine population was the Short-billed Dowitcher. Based strictly on percentages it would seem that quite a number of Short-billed Dowitchers are being removed by peregrines during the Dowitchers' spring migration. However, a closer look at the data reveals that a large number of these individuals were taken late in the breeding season (but prior to northward autumn migration), when any individuals present in the study area are likely to be stragglers (lost or ill birds). Because peregrines are known to exploit stragglers or anomalous individuals (White et al. 2002), it seems likely that these late-season Dowitchers are not representative of the total number of Dowitchers taken, and instead inflate these estimates.

The estimated impact of peregrine predation on Ruddy Turnstone populations (3.4% population removal) seems large and may warrant further studies, particularly

in areas where Ruddy Turnstones are considered rare or are known to be reliant on specific migration stopover sites.

Other than the species discussed here, there is no indication from our data that peregrines are having a significant impact on any of the other species of conservation concern present in the study area. In particular, Red Knots and Wilson's and Piping Plovers do not seem to be selected as prey at all (and if they are it is in small numbers), and American Oystercatchers are used in such small numbers that a significant direct impact from predation seems unlikely. However, it is important to point out that the presence of a peregrine with specialist tendencies toward any of these species could change this impact.

There is no doubt that this Peregrine Falcon population relies heavily on migrating shorebirds and waterbirds as a prey source. We estimate that peregrines are removing <1% of the migrating shorebirds and waterbirds that pass through this study area each spring. It seems unlikely that the presence of peregrines has a significant direct impact on these migrating birds.

In addition to the direct effect discussed here (predation), it is important not to discount the indirect effects of avian predators in this system. The presence of Peregrine Falcons in an area has been shown to have several indirect effects on prey species, including alteration of migration times of prey species (Ydenberg et al. 2004), reduction of foraging time and efficiency (Quinn 1997), or change in community structure in even more complex ways (Paine et al. 1990). While we did not study these indirect effects on the prey populations, we feel that any proposed

management action should consider these possibilities. In the case of the most conservation-sensitive species, specific studies of these effects may be warranted.

Although peregrines have been removed from the Federal Endangered Species list, they remain a threatened species in Virginia and are threatened or endangered in most neighboring states. One of the driving factors in the decision to introduce peregrines into this area was the abundance of prey, mainly in the form of shorebirds and waterbirds (Barclay 1988). If only the preservation of this species is taken into account, then the decision seems to have been wise. During our study no young died from malnutrition or seemed to otherwise suffer from a lack of food. There was no evidence of inter-sibling aggression that would indicate a shortage of food, nor was there evidence that food is a limiting factor in the establishment of new territories. In fact, nest sites here are often quite close together (<5km apart in some cases), and birds have been reported attempting to establish additional nest territories where no suitable nesting substrate exists. From the standpoint of the Peregrine Falcon, this seems to be a clear conservation success story. However, the conservation of the entire avian community is considerably more complicated.

There is certainly no straightforward resolution to the types of conservation conflicts brought about when a conservation-sensitive predator utilizes conservation-sensitive prey. In this particular case, the life history strategies of the species involved makes direct assessment of interactions and impacts difficult. We believe that this bioenergetics approach provides not only a reasonable estimate of the energy demands of extant populations, but can also be scaled to accommodate future

demographic changes. When combined with information on prey usage, it becomes possible to evaluate some of these impacts and guide future studies.

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## APPENDIX

Table 2. Species used as prey items by Peregrine Falcons during the 2004 and 2005 breeding seasons in Virginia. Species were identified using Digital Video Recording (DVR) or by prey remains collected from the nest site. Each species was grouped into passerines (PASS), migrating shorebirds (MISH), breeding shorebirds (BRSH), woodpeckers (PECK), terns (TERN), herons and egrets (HERON), rails (RAIL), ducks (DUCK), or gulls (GULL). Columns labeled DVR(%) and COLL (%) refer to the number of individuals identified and the percentage of that species of the prey total identified by DVR and by prey remains collections, respectively. Columns labeled DVR BM (%) and COLL BM (%) list the biomass conversions in grams and the percentage of total biomass for species identified by DVR and by prey remains collections, respectively. Biomass data was taken from Dunning (1993).

SPECIES	GROU P	DVR (%)	DVR BM(%)	COLL. (%)	C BM(%)
<i>American Black Duck</i>	DUCK	0 (0)	0 (0)	1 (0.19)	280 (0.40)
<b>Anas rubripes</b>					
American Green-winged Teal	DUCK	0 (0)	0 (0)	1 (0.19)	318 (0.45)
<b>Anas crecca</b>					
American Crow <b>Corvus brachyrhynchos</b>	PASS	3 (0.52)	1344 (5.33)	2 (0.37)	896 (1.27)
American Oystercatcher <b>Haematopus palliatus</b>	BRSH	1 (0.17)	500 (1.98)	2 (0.37)	1264 (1.79)
American Robin <b>Turdus migratorius</b>	PASS	2 (0.35)	154.6 (0.62)	1 (0.19)	77.3 (0.11)
Baltimore Oriole	PASS	0 (0)	0 (0)	1 (0.19)	33.75 (0.05)

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<b>Icterus galbula</b>					
Black-crowned Night-Heron <b>Nycticorax nycticorax</b>	HERO N	0 (0)	0 (0)	1 (0.19)	883 (1.25)
Brown-headed Cowbird <b>Molothrus ater</b>	PASS	0 (0)	0 (0)	7 (1.3)	307.3 (0.43)
Blue Grosbeak <b>Passerina caerulea</b>	PASS	3 (0.52)	85.2 (0.33)	2 (0.37)	56.8 (0.08)
Blue Jay <b>Cyanocitta cristata</b>	PASS	7 (1.21)	607.6 (2.4)	43 (8.0)	3732.4 (5.27)
Bobolink <b>Dolichonyx oryzivorus</b>	PASS	0 (0)	0 (0)	2 (0.37)	84.1 (0.12)
Brown Thrasher <b>Toxostoma rufum</b>	PASS	0 (0)	0 (0)	1 (0.19)	68.8 (0.10)
Boat-tailed Grackle <b>Quiscalus major</b>	PASS	2 (0.35)	333 (1.32)	1 (0.19)	166.5 (0.24)
Carolina Chickadee <b>Poecile carolinensis</b>	PASS	0 (0)	0 (0)	1 (0.19)	21 (0.03)
Cedar Waxwing <b>Bombycilla cedrorum</b>	PASS	0 (0)	0 (0)	3 (0.56)	95.55 (0.15)
Clapper Rail <b>Rallus longirostris</b>	RAIL	11 (1.90)	3267 (12.95)	33 (6.16)	9801 (13.85)
Common Grackle <b>Quiscalus quiscula</b>	PASS	36 (6.22)	4086 (16.20)	62 (11.57)	7037 (9.94)
Common Tern <b>Sterna hirundo</b>	TERN	*SEE UTE	*	4 (0.75)	480 (0.68)
Common Yellowthroat <b>Geothlypis trichas</b>	PASS	0 (0)	0 (0)	1 (0.19)	10.1 (0.01)
Downy Woodpecker <b>Picoides pubescens</b>	PECK	0 (0)	0 (0)	4 (0.75)	108 (0.15)
Dunlin	MISH	1 (0.17)	46.9 (0.18)	23 (4.29)	1078.7 (1.52)

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<b>Calidris alpina</b>					
Eastern Bluebird <b>Sialia sialis</b>	PASS	0 (0)	0 (0)	3 (0.56)	97.8 (0.13)
Eastern Meadowlark <b>Sturnella magna</b>	PASS	0 (0)	0 (0)	2 (0.37)	178 (0.25)
European Starling <b>Sturnus vulgaris</b>	PASS	0 (0)	0 (0)	4 (0.75)	329.2 (0.47)
Fish Crow <b>Corvus ossifragus</b>	PASS	1 (0.17)	285 (1.13)	6 (1.12)	1710 (2.42)
Forster's Tern <b>Sterna forsteri</b>	TERN	*SEE UTE	*	23 (4.29)	3634 (5.13)
Gray Catbird <b>Dumetella carolinensis</b>	PASS	2 (0. 35)	74 (0.29)	0 (0)	0 (0)
Greater Yellowlegs <b>Tringa melanoleuca</b>	MISH	1 (0.17)	171 (0.68)	5 (0.93)	855 (1.20)
Killdeer <b>Charadrius vociferus</b>	BRSH	2 (0.34)	193 (0.77)	19 (3.55)	1833.5 (2.59)
Laughing Gull <b>Larus atricilla</b>	GULL	3 (0.59)	700 (2.77)	8 (1.49)	2600 (3.67)
Little Blue Heron <b>Egretta caerulea</b>	HERO N	0 (0)	0 (0)	1 (0.19)	339.5 (0.48)
Least Sandpiper <b>Calidris minutilla</b>	MISH	0 (0)	0 (0)	1 (0.19)	23.2 (0.03)
Least Tern <b>Sterna antillarum</b>	TERN	0 (0)	0 (0)	1 (0.19)	43.1 (0.06)
Lesser Yellowlegs <b>Tringa flavipes</b>	MISH	2 (0.35)	162 (0.64)	25 (4.66)	2025 (2.86)
Marbled Godwit <b>Limosa fedoa</b>	MISH	0 (0)	0 (0)	1 (0.19)	255.5 (0.36)
Marsh Wren <b>Cistothorus palustris</b>	PASS	0 (0)	0 (0)	1 (0.19)	11.25 (0.02)

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Mourning Dove <b>Zenaida macroura</b>	PASS	23 (3.97)	2737 (10.85)	4 (0.75)	476 (0.67)
Northern Cardinal <b>Cardinalis cardinalis</b>	PASS	0 (0)	0 (0)	3 (0.56)	133.95 (0.19)
Orchard Oriole <b>Icterus spurius</b>	PASS	0 (0)	0 (0)	2 (0.37)	39.2 (0.05)
Pectoral Sandpiper <b>Calidris melanotos</b>	MISH	0 (0)	0 (0)	1 (0.19)	81.4 (0.12)
Prairie Warbler <b>Dendroica discolor</b>	PASS	0 (0)	0 (0)	1 (0.19)	7.65 (0.01)
Purple Martin <b>Progne subis</b>	PASS	1 (0.17)	56 (0.22)	0 (0)	0 (0)
Rose-breasted Grosbeak <b>Pheucticus ludovicianus</b>	PASS	0 (0)	0 (0)	1 (0.19)	45.6 (0.06)
Red-bellied Woodpecker <b>Melanerpes carolinus</b>	PECK	0 (0)	0 (0)	4 (0.75)	246.8 (0.35)
Red-headed Woodpecker <b>Melanerpes erythrocephalus</b>	PECK	0 (0)	0 (0)	1 (0.19)	71.6 (0.1)
Red-eyed Vireo <b>Vireo olivaceus</b>	PASS	1 (0.17)	17 (0.07)	0 (0)	0 (0)
Rock Pigeon <b>Columba livia</b>	PASS	5 (0.86)	1772.5 (7.03)	3 (0.56)	1063.5 (1.50)
Ruddy Turnstone <b>Arenaria interpes</b>	MISH	21 (3.63)	2415 (9.57)	29 (5.41)	3335 (4.71)
Red-winged Blackbird <b>Agelaius phoeniceus</b>	PASS	0 (0)	0 (0)	1 (0.19)	52.55 (0.07)
Sanderling <b>Calidris alba</b>	MISH	0 (0)	0 (0)	4 (0.75)	228 (0.32)

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Short-billed Dowitcher <b>Limnodromus griseus</b>	MISH	13 (2.25)	1469 (5.82)	61 (11.38)	6893 (9.74)
Semipalmated Plover <b>Charadrius semipalmatus</b>	MISH	0 (0)	0 (0)	7 (1.3)	327.25 (0.46)
Semipalmated Sandpiper <b>Calidris pusilla</b>	MISH	3 (0.52)	93.9 (0.37)	13 (2.42)	406.9 (0.58)
Spotted Sandpiper <b>Actitis macularia</b>	MISH	1 (0.17)	40 (0.16)	0 (0)	0 (0)
Sparrow spp. <i>Emberizidae</i> spp.	PASS	0 (0)	0 (0)	1 (0.19)	16 (0.02)
Summer Tanager <b>Piranga rubra</b>	PASS	1 (0)	28.2 (0.11)	7 (1.3)	197.4 (0.28)
Plover spp. <i>Charadrius</i> spp.	USH	1 (0.17)	115 (0.46)	1 (0.19)	46.75 (0.07)
Tern spp. <i>Sterna</i> spp.	TERN	14 (2.42)	1590 (6.3)	* SEE COTE, FOTE	*
Virginia Rail <b>Rallus limicola</b>	RAIL	0 (0)	0 (0)	9 (1.68)	737.55 (1.04)
Warbler spp. <i>Parulidae</i> spp.	PASS	0 (0)	0 (0)	2 (0.37)	22 (0.03)
Willet <i>Catoptrophorus</i> <i>semipalmatus</i>	BRSH	12 (2.07)	2580 (10.23)	63 (11.75)	13545 (19.14)
Yellow-breasted Chat <b>Icteria virens</b>	PASS	0 (0)	0 (0)	2 (0.37)	50.6 (0.07)
Yellow-billed Cuckoo <b>Coccyzus americanus</b>	PASS	0 (0)	0 (0)	9 (1.68)	576 (0.81)
Yellow-shafted Flicker <b>Colaptes auratus</b>	PECK	0 (0)	0 (0)	11 (2.0)	1452 (2.05)
Unknown	U	405 (69.95 )	NA	0 (0)	0 (0)



## VITA

## Elizabeth Claire Long

Elizabeth Claire Long was born December 15, 1973 in Roanoke, Virginia. She graduated with an Advanced Studies degree from Cave Spring High School (Roanoke, Virginia) in June of 1991. She received her B. A. in Biology from the University of Richmond (Richmond, Virginia) in May of 1995.

Elizabeth entered the College of William and Mary in the Fall of 2003 as a graduate student in Biology and an affiliate of the Center for Conservation Biology. She defended her thesis in April of 2009. She is currently a Ph. D. candidate in Ecology at the University of California Davis.