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Great Blue Heron Predation on Stocked Rainbow Trout in an Arkansas Tailwater Fishery

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Abstract.—Fisheries managers seldom have adequate information to assess their stock losses to avian piscivores, which function as apex predators in many aquatic food webs. Our primary objective was to estimate the number of stocked rainbow trout *Oncorhynchus mykiss* consumed by great blue herons *Ardea herodias* on the Bull Shoals and Norfork tailwaters of north-central Arkansas. Between November 2000 and December 2001, we periodically surveyed great blue herons along 150.7 river km on the tailwaters of the Bull Shoals and Norfork dams. Heron density (number/km) in or along the river ranged from 0 to 4/km per survey, with the highest mean number located near the Bull Shoals Dam (2.31 herons/km). We recorded 467 prey captures by herons during 202 observation hours. Sculpin *Cottus* spp. were the most common prey ($N = 120$). Most prey (87%) measured 14 cm or less in length, and most captured live trout (85.4%) fell between 10.5 and 28.0 cm in length. While live trout represented only 48 of 359 identifiable prey items (13%), they comprised an estimated 62.8% of heron diet biomass. We developed a bioenergetics model that combined our observations with published metabolic coefficients and relationships to estimate heron energy demand during breeding and nonbreeding seasons. This analysis revealed that trout comprised an estimated 67% of heron daily energy demand in the study area. Heron daily energy demand peaked during the breeding season (March–May). Based on a mean monthly population estimate of 227 great blue herons requiring 156 million kJ of total energy/year, we calculated that herons consumed just under 50,000 catchable-sized stocked trout annually. This loss to great blue herons represents an estimated 2.4% of the approximately 2 million trout stocked in the study area. Thus, great blue heron predation likely represents only a minor source of trout mortality in the Bull Shoals and Norfork tailwaters.

Avian predation on fish stocks has received considerable attention due to the potential for substantial economic losses to fisheries (e.g., Pitt and Conover 1996; Glahn et al. 1999; Collis et al. 2002; Glahn and Dorr 2002). Depending on the system, piscivorous birds may have minimal (e.g., Draulans 1988; Suter 1995; Glahn et al. 2000, 2002) or highly detrimental effects on natural and artificial fisheries (e.g., Furness 1978; Matkowski 1989; Collis et al. 2002). In addition, it is often unclear whether fish losses due to avian predation are additive or compensatory with angler harvest or other sources of mortality (Wood 1987; Derby and Lovvorn 1997). Intensive studies in areas with high piscivorous bird densities are necessary to realistically assess the effect of avian predation on freshwater fish stocks (Draulans 1988).

Fish consumption by avian piscivores has been quantified using bioenergetics models (e.g., Cairns et al. 1991; Glahn and Brugger 1995; Madenjian and Gabrey 1995; Derby and Lovvorn 1997). This approach typically incorporates estimates of the metabolic rate of predators using mass and temperature-specific equations developed by Kendeigh et al. (1977) and Furness (1978), and empirical data on predator diet and population size (Madenjian and Gabrey 1995; Derby and Lovvorn 1997; Pitt et al. 1998). However, to our knowledge, this approach has not been used to estimate fish losses to great blue herons in a natural riverine system. Bioenergetic models of consumer popu-

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lations typically estimate food consumption rates by combining individual energy demands and population size. This approach is more accurate than estimating predator effects based only on predator density and feeding rate. For example, bioenergetic models can incorporate variances in metabolic rate due to climatic factors, predator size, activity patterns, and prey energy density (Kendeigh 1970; Birt-Friesen et al. 1989). Pitt et al. (1998) demonstrated that such modeling approaches can represent an accurate estimator of consumption rates by free-ranging birds. However, site-specific analyses that focus on the predator population size, predator–prey habitat overlap, and predator diet are critical to the development of accurate fish loss estimates with a minimum of biases (Draulans 1988). Where the costs of long-term behavioral studies are prohibitive, modeling represents a desirable alternative for estimating the impacts of avian predators on commercial fish stocks.

Almost 2 million trout, mostly rainbow trout *Oncorhynchus mykiss*, are stocked annually in the Bull Shoals and Norfork tailwaters on the upper White River, Arkansas (Todd et al. 1998). Although managed as a put-and-take fishery, recent creel surveys have suggested that anglers harvest only 38% of the fish stocked in the tailwaters (Todd et al. 1998). The tailwaters support a variety of piscivorous birds, including raptors Accipitridae, kingfishers Alcedinidae, gulls Laridae, mergansers Anatidae, and herons Ardeidae. In particular, great blue herons *Ardea herodias* are both abundant in White River tailwaters and effective at stalking and capturing fish because of their unique morphology and foraging mode (Butler 1992). Furthermore, due to their relatively large size and high energy density, trout represent an energetically profitable prey item (Stephens and Krebs 1986) and, when available, may be a major component in great blue heron diets (Alexander 1977; Glahn et al. 1999). Our objective was to estimate the proportion of stocked trout consumed by great blue herons in these tailwaters. We developed a bioenergetics model that incorporated population size, local diet composition, breeding parameters, and species-specific physiological parameters. Also, we evaluated geographical and temporal variation in trout predation rates and discuss the possible management implications of our results for the trout fishery.

Study Site

Our research was conducted on the tailwaters of the Bull Shoals and Norfork dams along the upper White River in north-central Arkansas (Figure 1). The main portion of the study area consists of three contiguous sections of the Bull Shoals tailwater. The upper section (49.1 km) begins at the Bull Shoals Dam and continues down to the mouth of the Buffalo River at Buffalo City, Arkansas. The middle section (47.5 km) begins at Buffalo City and ends at Calico Rock, Arkansas. The lower section (48.0 km) runs from Calico Rock to Guion, Arkansas. The Norfork River constitutes a fourth study section (6.1 km) running from the Norfork Dam to the main tributary of the Bull Shoals tailwater at Norfork, Arkansas.

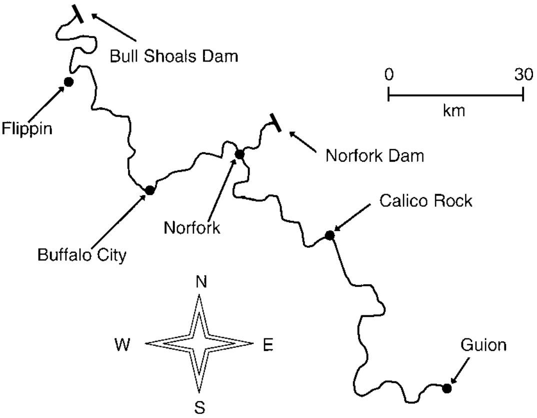

FIGURE 1.—Study area, including the Bull Shoals tailwaters (running from the Bull Shoals Dam to Guion, Arkansas) and the Norfork tailwaters (running from the Norfork Dam to the Bull Shoals tailwaters) (Todd et al. 1998). Temperature data were collected in Flippin, Arkansas. The remaining filled-in circles indicate the endpoints of river study segments (see Methods).

This section of the White River is used heavily for recreational fishing and boating. Nearly 2 million trout between 22.5 and 27.5 cm are stocked throughout the year along the entire length of the tailwaters of the dams (Todd et al. 1998). Rainbow trout harvest is not regulated by length limits, so the species constitutes a put-and-take fishery. River stage heights fluctuate irregularly and unpredictably in the tailwaters due to unscheduled hypolimnetic water release for hydroelectric generation from the Bull Shoals and Norfork Dams. Dam discharges range from 0.3 to 849.5 m^3/s.

Methods

Great blue heron population surveys.—Both wintering and resident great blue herons are present within the study area. We conducted population surveys of great blue herons by boat (MELPR 1998) within the three sections of the

Bull Shoals tailwater and on the Norfork tailwater. We completed a total of 50 surveys between November 2000 and December 2001. Each survey involved sampling a subsection of at least 8 river km in one of the four defined study segments: the upper, middle, and lower sections on the main tributary of the White River, and the Norfork River (Figure 1). The starting points for each subsection were located at 16 boat access points along the length of the river. We arbitrarily selected a starting point for the initial survey in each study segment and sequentially rotated the starting points of surveys within each of the four sections of the river for all subsequent surveys. We tried to sample the entire study area, but small sections of the river (approximately 2 km total) remained shallow ($<$30 cm) throughout the study and were thus inaccessible by boat and never surveyed. Surveys were conducted within each section approximately 3–4 weeks apart when water conditions permitted. We did not conduct surveys when the maximum river depth was less than 30 cm because the river was not navigable at these depths.

The survey start times varied between 0745 and 1830 hours to minimize potential time-of-day biases. Two observers counted all herons visible along the survey route, including birds that were foraging, perching in trees, resting, preening, nesting, and in flight. Because we observed birds on the river engaging in all the activities and behavior types exhibited by the great blue heron (Brandman 1976; Butler 1992), we assumed that the herons using the tailwaters stayed within visual range of the river throughout much of the diurnal period. Thus, we suggest that these surveys represent a reasonably accurate estimate of the density (number/km) of great blue herons dependent on the tailwater system. We estimated section-specific heron densities by dividing the number of herons observed by the number of river kilometers sampled. To minimize the chance of counting individuals more than once, we recorded the direction in which the birds moved and subtracted a bird from the final tally for each bird that moved ahead of us during the survey.

We used a one-way analysis of variance (ANOVA) to test for differences in great blue heron density due to time-of-day effects. We divided the day into twelve 1-h time blocks between 0700 and 1900 hours for this test. We also tested for differences in the mean number of great blue herons present in each of the four study sections, again using a one-way ANOVA. Significance was determined at an alpha-level of 0.05.

Great blue heron diet.—We observed foraging herons using 15–60× spotting scopes at 13 different river access points along the entire study area. We chose an initial foraging observation point arbitrarily, and if herons were present, sampling would take place there. If herons were not present, the next closest observation location was used. This pattern was repeated until we located foraging herons, at which time one observer recorded the behavior of an individual bird as long as it was visible or until it left the observation area. If more than one heron was visible at any given time, preference was given to foraging individuals over those individuals resting or preening to maximize the data on prey items captured and consumed. The observations were conducted between dawn and dusk to sample the entire diurnal period.

Great blue herons may forage nocturnally (Brandman 1976; Black and Collopy 1982; Rojas et al. 1999), but due to visibility constraints we could only identify prey and estimate the size of prey during daylight hours. Diel patterns have been observed in a number of fish species (e.g., Sjöberg 1989; Heggenes et al. 1993), so shifts in prey availability could alter great blue heron diets where nocturnal foraging occurs (McNeil et al. 1993). The nocturnal foraging patterns among great blue herons are varied; in some systems the rate of nocturnal foraging activity is equal to the rate of diurnal foraging activity (Black and Collopy 1982), while in other systems nocturnal foraging in great blue herons is absent (Gawlik 2002). The occurrence of nocturnal foraging has been correlated with tidal patterns in salt marsh habitat (Black and Collopy 1982) and tidal tributaries in riverine systems (Austin 1996). Austin (1996) suggested that bottom-dwelling prey species were only available during low tides, thus prey availability influenced nocturnal foraging patterns in great blue herons. McNeil et al. (1993) monitored nocturnal activity patterns in a riverine lake formed by a widening in the St. Lawrence River. The great blue herons using this system were not exposed to tidal cycles, and nocturnal activity accounted for 63% of the rate of diurnal activity (McNeil et al. 1993), suggesting that nocturnal foraging may be important in some nontidal areas. We do not know if great blue herons forage nocturnally in our study area. To our knowledge, the extent of nocturnal foraging in great blue herons using lotic, nontidal habitats has not been examined. Great blue herons are visual foragers (Kushlan 1978), and prey detectability for fish-eating birds is directly influenced by water transparency (Eriksson 1985). Thus, we suggest that the importance of nocturnal foraging in this population is likely minimal due to the availability of shallow, transparent water as foraging habitat for wading birds throughout the diurnal period. Additionally, our data collection emphasized the proportions of different prey types in the great blue heron diet and suggest that the lack of nocturnal observations should only nominally impact our estimate of heron energy intake (which was estimated from heron bioenergetics as described below). Our estimates would be measurably affected only if the great blue herons did substantial nocturnal foraging (which we believe is unlikely in our system) and if the diet composition is dramatically different between night and day (which is unknown). For our modeling analysis, we assumed that the proportions of prey items in the diet would be similar during diurnal and nocturnal foraging bouts.

We estimated the proportion of various prey items consumed by foraging herons by recording the number and frequency of all successful prey captures. We identified prey type through a spotting scope as herons take several seconds to manipulate prey before swallowing. For all successful captures, we classified prey into one of the following categories: shad (family Clupeidae); trout (family Salmonidae); dace, shiners, and minnows (family Cyprinidae); suckers (family Catostomidae); darters (family Percidae); sculpins (family Cottidae); or ‘‘other.’’ ‘‘Other’’ prey items included frogs, salamanders, snakes, and crayfish. We distinguished live, viable trout versus dead trout and/or cleaned-trout parts discarded by anglers. Trout parts could be clearly identified based on shape and color, and dead trout were distinguished by an obvious lack of movement following capture. We estimated the consumption rates of various prey items both in terms of the percent frequency of total prey items taken and the percent biomass consumed.

To estimate size, we used heron culmen length as a reference (14 cm; e.g., Bayer 1985; Parkhurst et al. 1992; Pitt et al. 1998) and recorded prey lengths to the nearest one-quarter bill length (3.5 cm). Some prey items were too small to identify and were recorded as having lengths of less than 3.5 cm. We estimated the foraging depth used by great blue herons during successful captures using the herons’ legs as a reference. One museum specimen from Arkansas State University was used to determine heron leg length; tarsus length was measured at 19.6 cm, and the distance between the ankle and knee joints was measured at 23.0 cm. Butler (1992) reported standard deviations in the measurement of great blue heron tarsus lengths from British Columbia (males: 165.9 ± 6.7 mm [mean ± SD]; $N = 24$; females: 152.0 ± 7.0 mm; $N = 29$) and Nova Scotia (males: 178.7 ± 11.6 mm; $N = 16$; females: 170.8 ± 12.2 mm; $N = 15$). These reported tarsus lengths vary by only 4–7%. Because there is relatively little variation in heron tarsus length, we used our measurement of tarsus length to classify foraging depths into several categories. For example, we recorded water depths at one-quarter tarsus length $\cong$ 5 cm, one-half tarsus length $\cong$ 10 cm, or 1 tarsus length $\cong$ 20 cm. A variation in tarsus length of about 1 cm should not have affected the accuracy of estimating water depth in these lower precision depth intervals.

Bioenergetic model.—We developed a model of the bioenergetic demand for the great blue heron population of the Bull Shoals and Norfork tailwater system (Table 1; Figure 2). We first estimated the individual basal-energetic demand for adult great blue herons. To determine the basic existence metabolic requirements for individual adult herons, we estimated metabolic rates for varying ambient temperatures. Temperature-specific existence metabolism for adult herons (ME) was based on the following equations (Kendeigh et al. 1977; Pitt et al. 1998):

$$\text{ME} = 24.179W^{0.50} \quad \text{at } 0°\text{C} \quad \text{and}$$

$$\text{ME} = 4.498W^{0.67} \quad \text{at } 30°\text{C},$$

where ME is existence metabolism (kJ/heron/d) and W is the mean mass of an adult great blue heron (g). We calculated mass-specific ME using an estimate for adult heron body mass (2,230 g; Butler 1992). The above equations represent two endpoints of a linear relationship between metabolism and temperature (Kendeigh 1969; Kendeigh et al. 1977; Pitt et al. 1998). The equation used to determine metabolic requirements, extrapolated from the above relationships, was as follows:

$$\text{ME} = -12.65T + 1167.3,$$

where T is temperature (°C). Mean monthly temperature data between the months of November 2000 and December 2001 were obtained from Weather Underground (2002). The weather data were collected in Flippin, Arkansas, located in the upper section of our study site (Figure 1). By employing these established relationships, our model should estimate individual great blue heron main-

TABLE 1.—Parameters used in a bioenergetic model of heron energy ration on the Bull Shoals and Norfork tailwaters in Arkansas during November 2000–December 2001.

Parameter	Value or source
Adult great blue heron population density	Population surveys (this study)
Mass of adult heron	2,230 g (Butler 1992)
Diet composition	Foraging observations (this study)
Prey energy value	7.3 kJ/g for rainbow trout (Bennett and Hart 1993; Pitt et al. 1998) 8.1 kJ/g for Clupeidae (Cummins and Wuycheck 1971) 7.2 kJ/g for Cyprinidae (Cummins and Wuycheck 1971) 6.2 kJ/g for Catastomidae (Cummins and Wuycheck 1971) 4.2 kJ/g for Percidae (Kitchell et al. 1977) 5.8 kJ/g for Cottidae (Cummins and Wuycheck 1971)
Heron assimilation efficiency	0.87 (Pitt et al. 1998)
Percent breeding adults	77% (Cairns et al. 1991; Madenjian and Gabrey 1995)
Clutch size	3.2 (Butler 1997)
Mortality of young	37.5% (Butler 1992)
Air temperature	Monthly average (Weather Underground 2002)

tenance energy demand during the nonbreeding season (Pitt et al. 1998). Given additional energy demands of free-ranging birds (Birt-Friesen et al. 1989), we assumed that another 30% of ME was required by wading birds to satisfy the energy requirements of great blue herons in the wild (Kushlan 1976; Butler 1993). This adjustment was used to estimate the daily basal-energetic demand for an individual adult great blue heron (Figure 2).

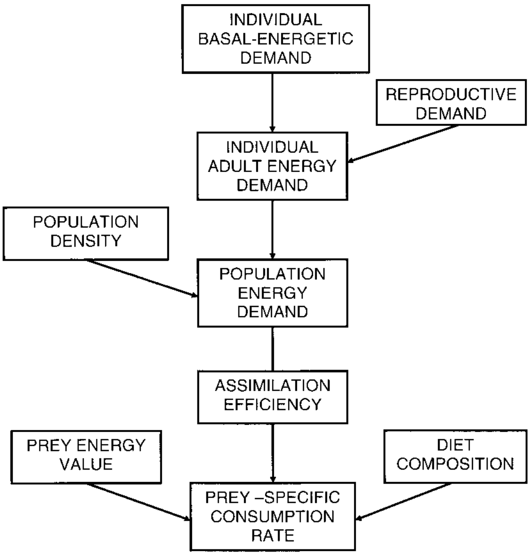

FIGURE 2.—Relationships of bioenergetic input variables to great blue heron energetic demand on the Bull Shoals and Norfork tailwaters during November 2000–December 2001. Individual basal-energetic demand represents the existence metabolism plus an additional 30% to reflect the food needs of individual adult great blue herons. Reproductive demand includes breeding variables (i.e., clutch size, chick survivorship, and growth rates). The figure was adapted from Kendeigh et al. (1977) and Furness (1978).

We incorporated the additional reproductive energy demand of breeding adults and nestlings during the breeding season (Table 1; Figure 2). Great blue herons begin laying eggs between February and May depending on latitude (James and Neal 1986; Butler 1992; Bennett et al. 1995). Egg laying date is relatively early in our study area due to the warmer ambient temperatures in our region; great blue herons have been observed nesting as early as the third week of February in Arkansas (James and Neal 1986). We first observed nestling great blue herons on 1 April 2001. Because the incubation period ranges from 25 to 30 d (Butler 1992, 1997), we assumed eggs were laid in early March. Great blue heron chicks reach full body mass after approximately 60 d (Bennett et al. 1995; Butler 1997). We calculated the additional breeding season energetic requirements for adults and the energy requirements of growing chicks during March, April, and May.

To our knowledge, the proportion of nonbreeding great blue heron adults has not been determined (Butler 1994; Madenjian and Gabrey 1995; Pitt et al. 1998). We applied an estimated proportion of nonbreeding adults developed by Cairns et al. (1991) for free-living, inshore seabird populations to our model (Madenjian and Gabrey 1995). Data on survivorship and age of first breeding were used to calculate the number of nonbreeders present (0.609) for each pair of breeding adults in a stable population (Cairns et al. 1991). Using this proportion, we calculated the percent of adult great blue herons that are likely to engage in breeding activities as 77%. We also assumed a

1:1 sex ratio (Fisher 1958). Heron clutch size generally increases with latitude within a range of 1–6 eggs (Butler 1992, 1997). Nesting herons from latitudes comparable to Arkansas have clutch sizes of 1.5 (Florida) to 3.2 (California; Pratt and Winkler 1985; Butler 1997). We used a latitude-dependent equation to determine an estimated clutch size of 3.2 for our study area (Butler 1997; Table 1). Based on Butler (1993), we assumed that adult female herons required an additional 155 kJ/d during the egg-laying period in addition to their basic metabolic requirements. This requirement was included over 6.4 d because females generally lay one egg every 2 d (Butler 1993). Finally, we assumed an egg failure rate of 47% based on data reported from comparable latitudes (Gill 1973; Pratt and Winkler 1985).

Further, we assumed that both parents assisted with feeding the nestlings (Butler 1993; Bennett et al. 1995) and thus shared the additional energetic requirements of brood rearing equally. The energetic demand for nestlings was estimated at 10-d intervals to adjust for growth and chick mortality (Bennett et al. 1995). Total energy requirements per average nestling until day 60 were taken from Bennett et al. (1995). The mean nestling survival rate for great blue heron nests was assumed to be 62.5% ($N = 8$ studies; Butler 1992). Because we did not determine daily nestling mortality rate in the local study area, we used this assumption to calculate 37.5% nestling mortality through the breeding period (Table 1). We divided this loss equally among six 10-d nestling growth periods (or a 6.25% loss of nestlings in each period), and adjusted nestling energy demand accordingly.

We estimated the great blue heron population density during population surveys (Table 1; Figure 2). Because the number of great blue herons using the river varied by month, we assumed that the size of the population using the system was dynamic. A dynamic population was expected because of mortality and the seasonal movement of migrants. When calculating energy demand, we used the mean population size for each month within each river segment. We then multiplied the energetic demand for an individual great blue heron by the estimated population size of herons on each section of the tailwaters to determine the total required energy intake for the population for each month. This yielded the daily population energy demand for the months that herons did not engage in nesting activities (Figure 2). For the months of March–June, we used the individual adult energy demand plus the additional energy requirements of chicks and breeding adults to estimate the energetic demand for the heron population during the breeding season (Figure 2).

TABLE 2.—Coefficients for regressions ($W = a \cdot L^b$) of wet weight (W) versus body length (L) of fish commonly consumed by great blue herons on the Bull Shoals and Norfork tailwaters during November 2000–December 2001. Range is range of masses of fish used in the development of length–weight relationships for the prey of great blue herons in north-central Arkansas.

Prey type	*a*	*b*	Range (*W*)
Clupeidae	0.0066	3.1982	1–147 g
Rainbow trout	0.01	3.0234	36–11,000 g
Cyprinidae	0.0133	2.8066	1–12 g
Catostomidae	0.0084	3.0983	9–327 g
Percidae	0.0317	2.5972	1–21 g
Cottidae	0.0086	3.3523	1–23 g

We next determined how much of the heron population energy demand would be fulfilled by trout consumption using the heron diet data (i.e., the estimated proportion of prey biomass comprised of trout). We determined the proportion of each prey type in the heron diet through our observational data and converted these to estimated energy values. For this estimate, we determined a mean biomass conversion factor for the prey items in the heron diet and multiplied this value by the consumption rates of those prey items based on the proportion of each prey type in the diet. The biomass of each prey item was estimated with length–weight relationships applied to the mean length of each prey type determined during foraging observations. As an estimate of the mean mass for trout, we used the length–weight relationship for lotic rainbow trout from Simpkins and Hubert (1996):

$$\log_{10}W = -5.023 + 3.024 \cdot \log_{10}\text{TL},$$

where W is mass in grams and TL is total length in millimeters. The trout parts obtained from angler cleaning practices were estimated to weigh 25% of a whole trout. To estimate the mass for fish other than trout, we used length–weight relationships based on the measurements of specimens from the Arkansas State University fish collection from Stone, Izard, and Baxter counties, Arkansas (Table 2). The mass estimates for prey items in each fish prey group included in the model were obtained from these relationships (Table 2) using the estimated lengths of the prey items that were consumed by great blue herons during foraging observations. The mass estimates based on the length–weight relationships allowed us to es-

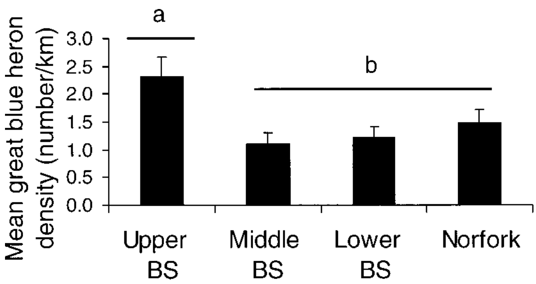

FIGURE 3.—Mean great blue heron densities recorded on surveys along the Bull Shoals (BS) and Norfork tailwaters during November 2000–December 2001. The upper section of the Bull Shoals tailwaters (a) had a significantly higher heron density than all other study sections (b) of the tailwater system (ANOVA: $F = 2.82$; df = 3, 50; $P = 0.049$). Error bars represent ±1 SE.

TABLE 3.—Mean number of great blue herons observed per river kilometer on the Bull Shoals and Norfork tailwaters by survey month during November 2000–December 2001. During each month, we conducted at least one survey in each of the four described study sections.

Month	Number of river km surveyed	Number of herons	Mean herons/ river km
Nov 2000	34.6	76	2.2
Dec 2000	17.7	47	2.7
Jan 2001	88.4	146	1.7
Mar 2001	179.9	401	2.2
Apr 2001	29.3	52	1.8
May 2001	33.6	60	1.8
Jun 2001	31.5	68	2.2
Jul 2001	40.2	29	0.7
Aug 2001	37.7	13	0.4
Sep 2001	23.5	34	1.5
Oct 2001	16.5	21	1.3
Dec 2001	21.7	26	1.2

timate the mean mass of each prey type consumed by great blue herons.

We multiplied the mass estimates by energy density to estimate the energy input provided by each prey type. We used an energy density estimate of 7.3 kJ/g wet weight (Bennett and Hart 1993; Pitt et al. 1998) for trout (Table 1). The values for Clupeidae (8.1 kJ/g), Cyprinidae (7.2 kJ/g), and Cottidae (5.8 kJ/g) were taken from Cummins and Wuycheck (1971). The energy density for Percidae (4.2 kJ/g) was taken from Kitchell et al. (1977). We could not find an energy density value specific to the Catastomidae family, so we used a general estimate for Osteichthyes (6.2 kJ/g) (Cummins and Wuycheck 1971). An assimilation efficiency of 0.87 was applied to all prey types (Pitt et al. 1998; Table 1).

We estimated the rainbow trout predation rate by great blue herons using the above energy-based mass requirements and applying them to the proportion of catchable-sized trout in the heron diet. We divided the energy requirements of all great blue herons by the energy content of the proportion of catchable-sized trout actually in the great blue heron diet to determine the mass of trout needed to fulfill those requirements (Figure 2). We then calculated the number of trout needed to meet this mass requirement, thus fulfilling the energetic demand for the entire great blue heron population supported by the White River tailwater system. This yielded the total estimated annual rate of predation on rainbow trout by great blue herons (Figure 2).

Results

Between 27 November 2000 and 3 December 2001, we counted individual great blue herons along 493 river km during 50 surveys throughout the Bull Shoals and Norfork tailwaters. Of these, we completed 14 surveys along the upper section of the Bull Shoals tailwaters, 11 surveys within the middle section, and 13 on the lower section. We were only able to complete five surveys by boat on the Norfork due to consistently low water levels. Four additional roadside surveys were also included for this section, but only 2.1 km of this 6.1 km river segment could be sampled from a vehicle during each of these surveys.

Heron densities ranged from 0.0 to 4.1 herons/km among individual survey events. Heron densities did not vary significantly by hour of day across study sections (ANOVA: $F = 0.45$; df = 11, 37; $P = 0.92$). However, heron densities were significantly higher near the Bull Shoals Dam ($\bar{x} = 2.31$ herons/km; Figure 3) than in the middle ($\bar{x} = 1.11$ herons/km) or lower ($\bar{x} = 1.22$ herons/km) sections or in the Norfork tailwaters ($\bar{x} = 1.48$ herons/km; ANOVA: $F = 2.82$; df = 3, 50; $P = 0.049$). We recorded the highest number of herons between November 2000 and June 2001 (Table 3). This period corresponds respectively to the winter and the nesting seasons of great blue herons in the study area.

We recorded 467 successful prey captures out of 828 recorded strike attempts (56.4% success) during 202 h of monitored heron foraging behavior. Most successful prey captures took place in depths of 20 cm or less (86.9%; Figure 4). More prey were consumed from the 20-cm depth category than from all other depths ($N = 86$). Herons used standing and walking slowly as foraging behaviors almost exclusively (Kushlan 1978). In standing behavior, the individual stands in one

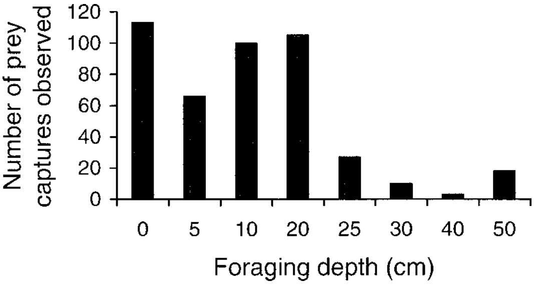

FIGURE 4.—Great blue heron foraging depths during successful prey captures on the Bull Shoals and Norfork tailwaters during November 2000–December 2001. Depths were estimated using the distance between heron leg joints as a reference. Based on measurements of a museum specimen, the distance between the toe and ankle joints = 19.6 cm and that between the ankle and knee joints = 23.0 cm. A depth value of 0.0 indicates that the foraging individual was not in the water. Deep-water captures resulting from plunging and jumping behaviors (Kushlan 1978) were recorded at depths of 50 cm.

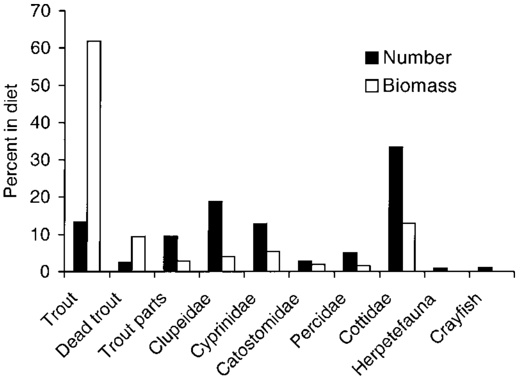

FIGURE 5.—Prey items consumed by great blue herons on the Bull Shoals and Norfork tailwaters during November 2000–December 2001. Proportions are calculated as percent of captures and diet biomass. Dead trout were those trout that did not move upon capture; trout parts were remains from angler catches and subsequent cleanings; $N = 359$ identifiable and successfully captured prey items.

place; walking slowly involves wading at a slow speed. Some prey captures, however, resulted from plunging and jumping foraging behaviors (Kushlan 1978), and the depths of these captures were estimated at 50 cm. These captures included trout ($N = 10$), dead trout ($N = 2$), trout parts ($N = 4$), sculpin ($N = 1$), and shad ($N = 1$).

We were able to identify 359 (76.9%) of the prey items from successful captures. The remaining prey items were either too small to facilitate identification (<3.5 cm), consumed too quickly for accurate identification, or obscured from the observer's view. Most prey items (71.9%) were fish other than trout including shad (19.2%); dace, shiners, and minnows (10.3%); suckers (2.9%); darters (5.2%); and sculpin (34.4%; Figure 5). Trout comprised 13.8% of the identifiable prey items ($N = 48$). Sculpin were the most common prey item comprising a total of 120 captures. Four crayfish (1.2%) were also captured during our observations. Additional prey items included one salamander, one frog, and one snake, none of which were identifiable to specific type. Shad are not normally present in the tailwater system, but we observed great blue herons feeding heavily on shad during a 2-d period following a fish kill event at the Bull Shoals Dam. In our study, most heron prey items that were clearly visible were less than 14.0 cm in length (Figure 6), and captured trout ranged from 3 to 39 cm in length. Of the 48 trout that were consumed during our observations, only 60.4% were of stocking size or larger (Figure 6). Most of the trout consumed by herons measured from approximately 10.5–28.0 cm (85.4%). The size-class of trout consumed most often by great blue herons measured approximately 21.0 cm ($N = 11$). We assumed that these represented the smaller stocked trout ($\bar{x}$ range = 22.5–27.5 cm; Todd et al. 1998). The trout that measured 14.0 cm or less ($N = 23$) were probably a combination of fingerling trout (stocked only nominally in the study area), and possibly trout from natural spawning events.

Live trout comprised 62.8% of the biomass consumed by great blue herons (Figure 5). Dead trout

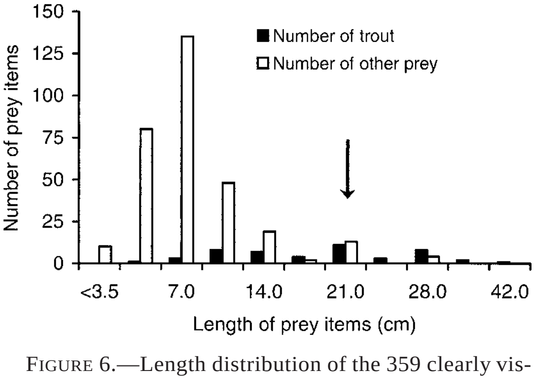

FIGURE 6.—Length distribution of the 359 clearly visible prey items consumed by great blue herons during foraging observations on the Bull Shoals and Norfork tailwaters during November 2000–December 2001. The minimum length of stocked trout was estimated at 21 cm ($\bar{x}$ = 22.5–27.5; Todd et al. 1998), which is indicated by the black arrow.

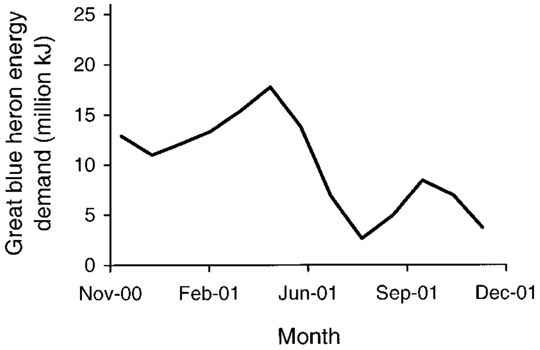

FIGURE 7.—Temporal variation in the estimated mean energy ration of the great blue heron population foraging on the Bull Shoals and Norfork tailwaters during November 2000–December 2001.

(including the carcasses of cleaned trout) made up 12.3% of the heron diet by the number of captures, and 12.5% of the diet by biomass. Although fish other than trout (shad, shiners, dace, minnows, suckers, darters, and sculpins) were numerically dominant in heron diets (71.9%), these fish comprise only 24.8% of the heron diet based on biomass. The biomass of the frogs, salamanders, snakes, and crayfish ($N = 7$) and of prey items less than 3.5 cm in length was considered negligible.

We estimated the energetic demand for the great blue heron population for each month of the study (Figure 7) and determined that great blue herons on the entire study site required an estimated 156×10^6 kJ of energy/year based on an individual consumption rate of 1,881 kJ/d and a mean population estimate of 227 individuals (this number varied monthly; Table 3). The peak monthly energy demand (18.2×10^6 kJ) for the great blue heron population on the Bull Shoals and Norfork tailwaters occurred during April 2001, which is the peak of the breeding period (Figure 7). We estimated that great blue herons foraging on the upper White River consumed 48,594 individual catchable-sized trout based on the proportion of stocked trout in the dietary biomass. This consumption represented approximately 2.4% of 2 million trout (22.5–27.5 cm in size) stocked annually in the Bull Shoals and Norfork tailwaters (Todd et al. 1998).

Discussion

Fish losses to avian piscivory surpass 50% in some systems (e.g., Derby and Lovvorn 1997), while in other systems losses to avian predation have appeared minimal (e.g., Madenjian and Gabrey 1995; Bur et al. 1997). Many fish rearing facilities have assessed the substantial economic losses due to the impacts of piscivorous birds (e.g., Parkhurst et al. 1992; Pitt and Conover 1996). Great blue herons can represent a troublesome predator at these facilities (Stickley et al. 1995; Andelt and Hopper 1996; Andelt et al. 1997), and substantial losses of trout have been documented (Parkhurst et al. 1992; Pitt et al. 1998; Glahn et al. 1999). In spite of this attention to the impacts of predation at fish rearing facilities, however, there have been few analyses of commercial fish losses to great blue herons in natural systems.

Madenjian and Gabrey (1995) found that the fish losses to great blue herons on Lake Erie were minimal compared with the losses due to walleye piscivory. Bur et al. (1997) similarly noted minimal impacts on Lake Erie's commercial fisheries due to predation by the double-crested cormorant *Phalacrocorax auritus*. The low rates of predation on reservoirs and lakes has been attributed to the presence of ample space in the water column and vegetative cover (Simmonds et al. 2000). Predator avoidance is more difficult in riverine systems, however, because ample volume and cover are not always available. Water releases from the Bull Shoals and Norfork dams, for example, have resulted in a scouring effect and have substantially reduced the presence of aquatic vegetation in our study area (Todd et al. 1998). Because predator avoidance may be more difficult in riverine systems, we might expect trout to constitute a higher proportion of great blue heron diets in tailwaters because of their relative vulnerability in this habitat. Our results indicated that trout were indeed an important component in great blue heron diets (13.4% of numbers, 61.8% of biomass). In spite of the profitability and prevalence of this prey type, however, great blue herons still obtained almost half of their diet from other sources.

In contrast to our findings, some picivorous birds have been reported to have substantial impacts on salmonid populations in riverine systems (Derby and Lovvorn 1997; Collis et al. 2002). Derby and Lovvorn (1997) found that double-crested cormorants and American white pelicans *Pelecanus erythrorhynchos* severely impacted the commercial fishery of the North Platte River in Wyoming. A bioenergetics model revealed that cormorants and pelicans on the North Platte River consumed up to 80% of the trout stocked during a single year (Derby and Lovvorn 1997). The differences between great blue heron and double-crested cormorant foraging modes and microhabitats may explain why herons did not feed more heavily on trout in our study area. Specifically, cormorants forage mainly while swimming and thus can exploit relatively deep water (up to 8 m) for their prey (Bur et al. 1997; Hatch and Weseloh 1999). Great blue herons, in contrast, forage almost exclusively in shallow (<0.5 m) and slow-moving water (Butler 1992).

Hom (1983) observed that foraging great blue herons preferred foraging depths of between 10 and 17 cm. Likewise, we found that great blue herons in the Bull Shoals and Norfork tailwaters primarily foraged in depths of less than 20 cm (Figure 4). Gawlik (2002) examined the numerical responses in wading birds at ponds with manipulated water depths and found that foraging birds not only fed preferentially from shallow depths but also incurred additional foraging costs at increased depths. As water depth increased, the prey density at which wading birds left a given foraging patch (the giving-up density) also increased (Gawlik 2002). In other words, deeper foraging patches were less profitable than shallower patches with the same prey density. Large trout seek refuge and prey at greater water depths in lotic systems (Kennedy and Strange 1982; Hill and Grossman 1993; Quinn and Kwak 2000), and smaller fish seek shallow habitats as velocity and aquatic piscivory refuges (Baltz and Moyle 1984; Harvey and Stewart 1991). Because great blue herons generally forage more efficiently in shallow water, trout may not be as vulnerable to great blue heron predation relative to some other avian predators that commonly forage in deep water.

In tailwater systems, fluctuations in water depth occur frequently and trout may become much more vulnerable to great blue herons and other wading birds at times of low discharge. Low water levels during the spring and summer months can also result in higher temperatures and low levels of dissolved oxygen, causing trout kills (Todd et al. 1998). Because great blue herons consume dead fish, some trout mortality due to low dissolved oxygen would probably be compensatory with great blue heron predation. Glahn et al. (2000) found that great blue herons preferred to feed on unhealthy as opposed to healthy catfish because unhealthy catfish were found closer to the surface of the water. If the levels of dissolved oxygen in tailwater systems cause trout to spend more time near the surface, those trout will become more vulnerable to wading bird predation. This effect would be enhanced by the reduced availability of deeper habitat as refugia for trout. Maintaining relatively high minimum flows in tailwater systems could reduce trout mortality by increasing dissolved oxygen levels, and by increasing available deepwater refugia from foraging wading birds.

We believe that our estimates of trout removal by great blue herons are reasonable; estimates from a similar modeling approach have compared favorably with direct estimates of the consumption rates of trout by great blue herons. Pitt et al. (1998) estimated the rate of trout consumption by free-ranging great blue herons at a hatchery using a similar bioenergetics model and compared this estimate with a direct estimate based on observed rates of food intake. Pitt et al. (1998) reported that monthly consumption rates predicted by bioenergetics modeling agreed with directly estimated consumption rates for 9 months of the year (October–May, July). The discrepancy between the two estimates during the remaining months was attributed to temporal changes in great blue heron abundance and the inaccuracy of population estimates (Pitt et al. 1998). We feel that our direct counts of great blue herons in the study area and direct foraging observations improved the accuracy of our consumption estimates based on the bioenergetic model.

Our trout consumption estimate assumed that all of the energy required by the herons in our study system was taken from river resources. Great blue herons nesting away from the study area may have traveled to the river to forage, which would add more herons to the system than we included in our model and, thus, our analysis would likely underestimate the amount of trout predated on the river. Conversely, the herons we counted on the river may also have foraged at farm ponds and other habitats away from the river. Because our model assumed that the entire great blue heron population was obtaining all of its energetic needs from the river, we likely overestimated the number of trout removed by herons if they spent any time foraging away from the river. Regardless, we propose that these potential biases are minimal and the model may actually provide an upper-bound estimate of trout consumption by herons.

Our bioenergetics model predicts that each individual adult heron requires, on average, approximately 1,881 kJ/d. This energy ration should be met by 301 g/d of fish based on a mean energy density of 6.25 kJ/g (Cummins and Wuycheck 1971). Other studies have reported comparable maintenance requirements of 300 g/d for great blue herons (Glahn et al. 1999, 2000). Pitt et al. (1998)

reported estimated maintenance requirements ranging from 127 g/d for nonbreeding individuals to 451 g/d for breeding individuals based on a similar modeling approach. Pitt et al. (1998) also suggested that estimated maintenance requirements above 300 g/d actually overestimated directly observed population-level consumption during the breeding season. However, if we were to apply the highest maintenance requirement for great blue herons reported by Pitt et al. (1998) to our population (451 g/d), the rainbow trout loss to herons in the White River tailwater system would still be only 7%. Thus, even if we estimate predation rates using assumptions that would exceed the estimates based on our data and would yield the ''worst-case'' rates of trout loss, the impacts of great blue heron predation still are relatively minimal.

Based on our best estimates of modeling parameters, our results suggest that the energy ration for great blue herons on our study site is approximately 156 million kJ/year, representing a relatively minor source of stocked trout mortality (~2.4%) on the Bull Shoals and Norfork tailwaters. Our results provide a link to a terrestrial apex predator in the food web of this coldwater system and further the understanding of the interactions between aquatic food resources and avian piscivores. Although avian predators may choose prey items based on energetic profitability (Stephens and Krebs 1986), the spatial distribution of suitable foraging habitat may play an important role in defining the impacts on prey populations as well. Our results suggest that a lack of spatial overlap between the great blue herons and the larger stocked trout may play a key role in determining the predatory impacts of these birds in the Bull Shoals and Norfork tailwater system. Investigating the abundance and availability of aquatic prey items within specific foraging microhabitats of predators would enhance our understanding of the proximate mechanisms that drive prey selectivity in piscivores and would better enable us to predict which systems are vulnerable to significant losses to avian predators.

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