WINTER SURVIVAL OF IMMATURE CANVASBACKS IN INLAND LOUISIANA

WILLIAM L. HOHMAN, National Biological Service, Southern Science Center, 700 Cajundome Boulevard, Lafayette, LA 70506-3152, USA
JOSEPH L. MOORE, National Biological Service, Southern Science Center, 700 Cajundome Boulevard, Lafayette, LA 70506-3152, USA
J. CHRISTIAN FRANSON, National Biological Service, National Wildlife Health Center, 6006 Schroeder Road, Madison, WI 53711, USA

Abstract: In spite of management efforts, population indices for canvasbacks (*Aythya valisineria*) declined during 1955–93. Since 1985, Catahoula Lake, located in central Louisiana, has attracted more wintering canvasbacks than any other site in North America. Canvasbacks are attracted to Catahoula Lake because of its consistent flooding regime and abundant below-ground plant foods, but are at risk of lead (Pb) toxicosis because of the high density of spent Pb shot contained in sediments. To estimate survival rates and determine sources and timing of mortality, we radiomarked 172 immature canvasbacks during winters 1991–94. Half of our sample had blood Pb concentrations ≥ 0.2 parts per million (ppm) at time of capture and were considered Pb exposed. Blood Pb concentrations of others (unexposed) were initially at background levels (i.e., Pb < 0.2 ppm). Year had no effect on canvasback survival ($P = 0.357$), but survival was positively related to body mass ($P = 0.014$) and negatively related to the interaction of blood Pb concentration and body mass ($P < 0.001$). Winter survival estimates for Pb-exposed immatures were lower ($P \leq 0.045$) than those for unexposed immatures in 1992–93 (0.569 vs. 0.815, respectively) and 1993–94 (0.578 vs. 0.923, respectively) but did not differ ($P = 0.34$) in 1991–92 (0.747 vs. 0.857, respectively) when Pb-exposed canvasbacks had greater body mass and lower blood Pb concentration. Causes of mortality were gunshot (31%), Pb toxicosis (16%), drowning in commercial fishing nets (6%), and unknown (47%). Survival estimates for Catahoula Lake canvasbacks, especially Pb-exposed individuals, were lower than those previously reported for immature females wintering in coastal Louisiana or Chesapeake Bay. Most immatures that were initially exposed to Pb apparently survived the winter; however, subsequent survival and performance of annual cycle events may have been affected because exposed birds weighed less than unexposed birds. We recommend that Pb exposure in waterfowl be periodically monitored and managers give priority to reducing Pb shot availability at concentration areas.

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Between 1955 and 1993, the canvasback breeding population fluctuated between 364,000 and 760,000 and showed a general decline of 0.6%/year (Hohman et al. 1995). Causes for this apparent decline are not well understood, but habitat loss and degradation, low rates of recruitment, a skewed sex ratio favoring males (i.e., differential survival of sexes [Nichols and Haramis 1980*a*]), and reduced survival of canvasbacks during their first year are considered important constraints on population growth of the species (Hohman et al. 1995). Survival of immatures, especially females, is of special concern because return rates for female canvasbacks breeding in southwestern Manitoba suggest that on average only 21% of females survive their first year (69% annual survival thereafter; Serie et al. 1992:550). Sources and timing of mortality for immatures have been studied during some segments of the annual cycle (e.g., prefledged young; C. E. Korschgen, Natl. Biol. Serv., LaCrosse, Wis., unpubl. data), but our understanding of factors contributing to reduced annual survival of immatures is incomplete. High survival by immature female canvasbacks wintering in Chesapeake Bay (Haramis et al. 1993) and coastal Louisiana (Hohman et al. 1993) led those investigators to conclude that mortality must occur during other periods of the annual cycle or at other wintering or staging sites.

Since 1985, Catahoula Lake has attracted more wintering canvasbacks than any other site in North America (Woolington and Emfinger

1989). The density of spent Pb shot in Catahoula Lake sediments is high compared with that in other winter or staging areas (Wills and Glasgow 1964; Louisiana Dep. Wildl. and Fish. [LDWF], Baton Rouge, unpubl. data). Mortality associated with ingestion of Pb shot (i.e., Pb toxicosis) has been well documented for dabbling (Anatini) but not diving (Aythyini) ducks wintering at Catahoula Lake (Yancy 1953, Wills and Glasgow 1964, Zwank et al. 1985). Prevalence of ingested shot varied among months and was higher in immatures than adults, but about 27% of all canvasbacks collected at Catahoula Lake in winter 1987–88 had Pb in their gizzards (Hohman et al. 1990*a*). The body mass of these birds, after accounting for age, monthly variation, and body size, was reduced. This led Hohman et al. (1990*a*) to speculate that if overwinter and annual survival probabilities of Louisiana canvasbacks were related to their relative body mass in winter as in Chesapeake Bay canvasbacks (Haramis et al. 1986), then survival probabilities of birds exposed to Pb may be reduced relative to those of unexposed individuals. Our objective, therefore, was to estimate survival and determine causes and timing of mortality for immature canvasbacks wintering at Catahoula Lake.

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STUDY AREA

Catahoula Lake was a large (12,150 ha), shallow basin situated on the Mississippi River floodplain. Water levels were managed under a joint agreement between the LDWF, Fish and Wildlife Service, and U.S. Army Corps of Engineers. Under this agreement, the lake was drained to 8.2–8.4 m mean sea level (msl) in summer to stimulate plant growth and gradually flooded to 9.0 m msl beginning 10 days before the start of the waterfowl hunting season to provide harvest opportunity. Water levels were further increased (1.4 m) in midwinter, after the waterfowl hunting season, to discourage use of the lake by dabbling ducks and thereby minimize their ingestion of Pb shot (Zwank et al. 1985).

Canvasback arrival at Catahoula Lake in early November coincided with flooding (Woolington and Emfinger 1989). First arrivals and last birds to depart were mostly females and immatures (Woolington 1993). Peak counts generally occurred in January when the proportion of males was highest (Woolington 1993). Most canvasbacks departed Catahoula Lake before mid-March.

Catahoula Lake was one of the most intensively hunted waterfowl areas in Louisiana (Wills 1965, Wycoff et al. 1972, Shealy 1982). About 500 permanent blinds were maintained on the lake with additional temporary blinds located around the lake's brushy perimeter and floated in open water. A 445-ha sanctuary was located in the center of the lake. Waterfowl hunting seasons of 30 days duration were continuous in winters 1991–92 (23 Nov–22 Dec) and 1992–93 (21 Nov–20 Dec) but split into 2 segments in winter 1993–94 (20–28 Nov, 13 Dec–2 Jan). Harvest of canvasbacks was prohibited in all years. Following the hunting season and increase in water level, the lake was fished commercially with trot lines and trammel, gill, and hoop nets.

METHODS

We captured canvasbacks at night using spotlights (Cummings and Hewitt 1964). We captured birds before, during the split between seasons, and after the waterfowl hunting season. We assigned age (first yr = immature, after first yr = adult) to individuals on the basis of plum-

age (Haramis et al. 1982) or cloacal characters (Hochbaum 1942). We measured body mass (±5 g), bill length from the commissural point to tip of nail (±0.1 mm), maximum bill width distal to nares (±0.1 mm), keel length (±0.1 mm), tarsal bone length (±0.1 mm), and body length (±0.5 cm) from the tip of the bill to the base of the middle rectrix with the bird held on its back.

We examined canvasbacks radiologically for presence of embedded and ingested shot (Perry and Geissler 1980). A blood sample was taken by jugular venipuncture, analyzed for protoporphyrin (Franson et al. 1986), and frozen. We later analyzed blood samples for Pb using graphite furnace atomic absorption spectrophotometry (DeStefano et al. 1991).

We implanted radio transmitters in the abdominal cavities of canvasbacks following Olsen et al. (1992). Transmitters were internal, had a minimum life-span of 90 days, and reception range of 6–10 km from ground to an airplane equipped with 4-element Yagi antennas and flying at an altitude of 300 m. Transmitters were equipped with mortality sensors (thermistors) and had a mass of approximately 20 g (<2% of body mass). Transmitters had unique frequencies in the 164–168 MHz range. The release site for radio-marked canvasbacks was within the sanctuary portion of Catahoula Lake.

We searched for radio-marked canvasbacks using aircraft (Gilmer et al. 1981) and standard triangulation procedures (White and Garrott 1990), and determined their status (alive or dead) from transmitter pulse rate. We recovered mortalities immediately after they were discovered (Kenward 1987). Monitoring ceased when radios reached their 90-day life-span. Salvaged carcasses were necropsied to determine cause of mortality.

We deployed radio transmitters in immatures of both sexes because we anticipated survival would be affected primarily by Pb exposure and exposure was highest in immatures (Hohman et al. 1990*a*). Justification for implanting radio transmitters in males and females was based on earlier studies that showed no effect of sex on relative physical condition (i.e., size-adjusted body mass, fat, or protein) or prevalence of ingested shot (index of Pb exposure) in canvasbacks wintering at Catahoula Lake (Hohman et al. 1990*a*, Hohman 1993). Blood Pb concentrations ≥0.2 ppm are considered above background levels (U.S. Dep. Inter. 1986), so we classified birds with initial blood Pb concentrations ≥0.2 ppm as exposed and all others as unexposed. We attempted to radiomark equal numbers of exposed and unexposed birds. Birds with protoporphyrin ≥40 μg/dL and/or metal densities noted radiographically in their gizzards were initially considered exposed until results from definitive blood Pb analyses were known. We excluded from the study canvasbacks that weighed <900 g or were diagnosed by attending veterinarians as showing clinical signs of Pb toxicosis.

We calculated survival estimates and 95% confidence intervals for canvasbacks with the Kaplan-Meier procedure (Kaplan and Meier 1958, Cox and Oakes 1984) as modified by Pollock et al. (1989*a*). We censored individuals from derivation of survival estimates when loss of transmitter signal occurred (Pollock et al. 1989*b*). We attributed signal loss to bird movements or transmitter failure and not mortality. We compared year-specific survival curves for exposed and unexposed immatures with pairwise log-rank tests (Pollock et al. 1989*a*). Pairwise log-rank tests also were used to test for differences in survival curves between exposed and unexposed birds.

We used analysis of covariance models (controlling for size as described below) with type III sums of squares to examine effects of sex, month, and Pb status (unexposed = 1, exposed = 2) on body mass (PROC GLM; SAS Inst. Inc. 1989). Comparisons between years were complicated by annual differences in time of capture and limited sample sizes in some months. So to test for year effects, we compared body masses of radio-marked immatures captured in December 1991–93 (model: body mass = sex, Pb status, yr, and all interactions). We also examined influence of year on November and December body masses of immatures captured in 1992–93 (model: body mass = sex, Pb status, month, yr, and all interactions). First, we subjected the correlation matrix of 5 structural measurements (bill width, and tarsal, keel, bill, and body lengths) to principal components analysis. For this analysis, we included all canvasbacks captured in Louisiana from 1988 to 1994 (n = 366 M [192 adults, 174 immatures] and 334 F [157 adults, 177 immatures]). The first principal component (PC1) accounted for 65% of the variance in the original measures, described positive covariation among all measures, and had factor loadings ranging from 0.39 to 0.49. We used

scores on PC1 as a measure of body size and, hence, as the covariate in models of body mass (SIZE; Hohman 1993). We used analysis of variance to test for annual differences in blood Pb concentrations (log transformed) of exposed and unexposed canvasbacks.

We used proportional hazards procedures (PROC LIFEREG; SAS Inst. Inc. 1989) to further examine the influence of blood Pb concentration, body mass, and year on canvasback survival. Year was entered as a class variable, and blood Pb concentration, body mass, and interaction of blood Pb concentration and body mass were covariates. The response hazard (i.e., no. of days until mortality) was log transformed and we used the log-normal distribution for our error term. Assuming that survival risks were similar throughout winter, we calculated exposure days from the day of release until the individual died or was censored (i.e., 90 days or final radiolocation). We used a stepdown approach to eliminate nonsignificant ($P > 0.05$) factors. Following Ankney and Alisauskas (1991:801), we used residuals from the regression of body mass on SIZE (body mass = 1,085 + 31.40[SIZE], 170 df, $r^2 = 0.202$, $P < 0.001$) to calculate size-adjusted values of body mass (ADJMASS) used in above analyses.

RESULTS

We radiomarked 172 immature canvasbacks (Table 1). Our radio-marked sample consisted of 86 exposed and 86 unexposed immatures. Blood Pb concentrations of exposed canvasbacks were lower ($F = 5.38$; 2, 80 df; $P = 0.006$) in winter 1991–92 than in winters 1992–93 and 1993–94, but did not vary among years in unexposed birds ($F = 2.66$; 2, 78 df; $P = 0.077$) (Table 1).

Body Mass

All models relating SIZE (covariate), sex, Pb status, month, or year to body mass of radiomarked canvasbacks were significant ($P < 0.001$). Size-adjusted body mass of females was greater than that of males in December 1991 ($F = 9.65$; 1, 17 df; $P = 0.001$), but we found no evidence of an effect of sex on body mass in winters 1992–93 or 1993–94 ($F < 3.27$; 1, 125 df; $P \geq 0.073$) (Table 1). Whereas Pb status apparently was unrelated to body mass in winter 1991–92 ($F = 0.15$; 1, 17 df; $P = 0.707$), exposed immatures were lighter (67–83 g) than unexposed birds in winters 1992–93 and 1993–94 ($F = 16.81$; 1, 125 df; $P \leq 0.001$). Size-adjusted body mass of canvasbacks in December was similar in all years ($F = 1.04$; 2, 55 df; $P = 0.362$). Immatures captured in December were heavier than those captured in November in winters 1992–93 and 1993–94 ($F = 29.33$; 1, 125 df; $P < 0.001$).

Winter Survival

We tracked individual canvasbacks an average of 67 days (range 4–90 days, median = 88 days). An average of 87% of radio-marked canvasbacks suspected to be alive were located in the immediate vicinity of Catahoula Lake on each flight. We censored 21 birds for ≥14 days (emigrated from the study area), but 11 of these subsequently returned to the site or were relocated elsewhere. We recorded 5 mortalities in winter 1991–92, 20 in winter 1992–93, and 7 in 1993–94. Causes of mortality (total n: n exposed/unexposed, n M/F) were gunshot (10: 5/5, 3/7), Pb toxicosis (5: 4/1, 2/3), drowning in commercial fishing net (2: 2/0, 2/0), and unknown (15: 13/2, 12/3). Initial blood Pb concentration of mortalities averaged ($\bar{x} \pm$ SE) 2.51 ± 0.45 ppm (range 0.02–7.16 ppm) compared with 0.72 ± 0.11 ppm (range 0.01–7.66 ppm) for nonmortalities.

There were no year-specific differences in survival curves of exposed and unexposed immatures ($\chi^2 \leq 1.71$, 1 df, $P \geq 0.21$). Winter survival estimates for immatures with blood Pb concentrations ≥0.2 ppm at time of capture were lower than those of unexposed immatures in all 3 winters, but differences were significant ($\chi^2 \geq 4.09$, 1 df, $P \leq 0.045$) in winters 1992–93 (0.569 vs. 0.815, respectively) and 1993–94 (0.578 vs. 0.923, respectively) only (Fig. 1).

Proportional hazards analysis also suggested that year had no effect on survival ($P = 0.357$), but survival was positively related to ADJMASS ($P = 0.014$) and negatively related to the interaction of blood Pb concentration and ADJMASS ($P < 0.001$). The final model was log(survival days) = −0.331 + 2.573(ADJMASS [g]) − 0.183(ADJMASS)(blood Pb concentration [ppm]).

DISCUSSION

Survival rates for Catahoula Lake canvasbacks, especially Pb-exposed individuals, were lower than estimates obtained for immature females wintering in coastal Louisiana (0.952 ± 0.065; Hohman et al. 1993) or Chesapeake Bay

Table 1. Initial body mass and blood lead (Pb) concentrations (parts per million [ppm]) of immature canvasbacks captured and marked with radio transmitters at Catahoula Lake, Louisiana, in winters 1991–94.

	Winter								
	1991–92			1992–93			1993–94		
Measurement	Dec	Jan	All	Nov	Dec	All	Nov	Dec	All
Body mass (g)									
Sex									
Male	1,091[a]	1,239		1,031	1,188		1,010	1,116	
SE	35	38		14	17		28	20	
n	13	8	21	41	8	49	16	21	37
Female	1,198			1,057	1,116		1,039	1,111	
SE	42			19	33		28	27	
n	9	0	9	29	7	36	10	10	20
Combined	1,145	1,239		1,044	1,153		1,024	1,113	
SE	26	38		10	27		17	16	
n	22	8	30	70	15	85	26	31	57
Pb status[b]									
Exposed			1,186			1,057			1,035
SE			29			15			17
n	14	3	17	33	11	44	11	14	25
Unexposed			1,198			1,140			1,102
SE			33			25			15
n	8	5	13	37	4	41	15	17	32
Blood Pb (ppm)									
Pb status									
Exposed			0.59			2.25			2.14
SE			0.37			0.21			0.27
n			8			41			32
Unexposed			0.09			0.06			0.08
SE			0.48			0.21			0.24
n			14			44			25

[a] Least squares mean based only on factors contributing ($P < 0.05$) to model.
[b] Pb status: unexposed = Pb < 0.2 ppm, exposed = Pb ≥ 0.2 ppm.

(range 0.833–0.930; Haramis et al. 1993). Lead exposure contributed to reduced survival of Catahoula Lake birds. Canvasbacks with elevated Pb levels at the time of capture had reduced survival relative to unexposed individuals. This was evident even though exposure rates of radiomarked birds after release were unknown and some individuals that were previously unexposed likely ingested Pb and thereby became exposed. Indeed, 1 immature that was unexposed at the time of capture subsequently died of Pb toxicosis. Only 5 of 32 mortalities were attributed to Pb toxicosis, but Pb exposure contributed directly or indirectly to additional mortalities. For example, although causes of mortality for 15 birds were unknown, all but 2 of these unknowns were initially Pb exposed. Recovery of 11 of these transmitters from the lake's brushy perimeter and, in 1 instance, from a tree cavity suggested predation by mink (*Mustela vison*), raccoon (*Procyon lotor*), or raptors. We suspect that movement patterns, behavior (e.g., feeding, flocking, locomotory activities), and use of habitat (open water vs. flooded emergent cover) differed between exposed and unexposed canvasbacks and may have made Pb-exposed birds more vulnerable to predation; however, salvaged remains were insufficient to enable us to distinguish scavenged carcasses (i.e., birds dying of other causes) from apparent predations.

Illegal shooting was an important source of mortality for immature canvasbacks at Catahoula Lake as it was at Chesapeake Bay (Haramis et al. 1993). Ten of 17 birds for which we were able to determine cause of mortality died of gunshot wounds. In addition, 59% of all mortalities were recorded during the 30-day hunting season (i.e., about 33% of the monitoring period). Likewise, 14 of 15 deaths documented during a 3-year study of canvasback survival in Chesapeake Bay (Haramis et al. 1993) and all 5 deaths observed in coastal Louisiana (Hohman et al. 1993) occurred during the duck hunting season. Although there were no year-specific differences in survival estimates, the number of hunter-killed birds varied among years. No hunting mortality was observed in winter 1991–92 because all radios were deployed after the hunting season. In winters 1992–93 and 1993–94, radio transmitters were deployed before the start of the waterfowl season, but while we observed no hunting mortalities in winter 1993–94, we documented 10 hunter kills in 1992–93.

The timing and framework of hunting seasons differed between winters 1992–93 (continuous season) and 1993–94 (split season), but we attribute apparent differences in hunting mortalities to annual variation in water levels and hunter effort. Water control capabilities at Catahoula Lake are limited. Local rainfall or backflooding of the Mississippi River caused by major runoff events upstream produce abrupt changes in lake levels. For example, in winter 1987–88, lake levels increased 3.9 m in 4 days following locally heavy rains. Hunting opportunity was associated with water levels because numbers of dabbling ducks using the lake decline and permanent blinds become inundated when water levels exceed 9.0 m msl. In winter 1992–93, water levels were held within 0.5 m of the target level throughout the hunting season, but in winter 1993–94 water levels were ≥0.5 m of target level on 20 of 30 hunt days. Consequently, waterfowl numbers and hunter success were re-

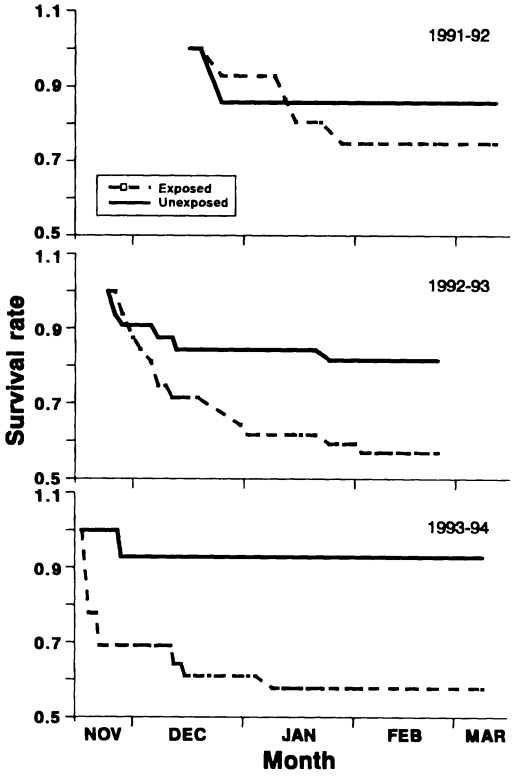

Fig. 1. Kaplan-Meier survival estimates for immature canvasbacks at Catahoula Lake, Louisiana, during winters 1991–94. Survival curves for immatures with blood lead (Pb) concentrations ≥0.2 parts per million (ppm) (exposed) at time of capture and immatures with blood Pb < 0.2 ppm (unexposed) differed ($P \leq 0.045$) in winters 1992–93 and 1993–94 only.

duced in winter 1993–94 compared with winter 1992–93 (LDWF, Baton Rouge, unpubl. data). If, as we suspect, hunting effort at Catahoula Lake was positively related to success and waterfowl numbers, then risks of hunting mortality probably were lower in winter 1993–94 than in winter 1992–93.

Hunting mortalities may have not been intentional but rather resulted from hunters not being able to distinguish canvasbacks from legal species. This was the case in a closed area on the upper Mississippi River near La Crosse, Wisconsin, where almost 41% of hunters encountering canvasbacks apparently misidentified birds and shot at them (Korschgen et al. 1993). Encounter rates with hunters have not been quantified for canvasbacks at Catahoula Lake but are likely high when water levels are low because of the high density of hunters, limited refuge area available to birds, canvasback feeding preferences for tubers of shallow-water emergent (arrowhead [*Sagittaria* spp.]) and moist-soil (chufa flatsedge [*Cyperus esculentus*]) plants (Hohman et al. 1990*b*), and dispersion of blinds relative to available shallow-water feeding areas. Moreover, increases in canvasback numbers at Catahoula Lake were recent (<10 yr; Woolington and Emfinger 1989), so hunters may have been unfamiliar with the species.

Ingestion of 1 Pb shot can be lethal to ducks (Sanderson and Bellrose 1986). Nonetheless, we documented winter mortality for only 28 of 86 immature canvasbacks that had elevated blood Pb levels at the time of capture. Susceptibility of waterfowl to Pb toxicosis is related to diet (Sanderson and Bellrose 1986). Susceptibility also may be influenced by the timing of exposure and relative body mass. The mediating effect of body mass on lethality of Pb exposure in canvasbacks was suggested by the positive coefficient for ADJMASS in the final proportional hazards model. Lead retention rates are unknown for free-ranging ducks, but blood Pb or protoporphyrin concentrations remained elevated in captive canvasbacks and ring-necked ducks (*Aythya collaris*) for 4–7 weeks after experimental dosing (Franson et al. 1986, Mautino and Bell 1986). While blood Pb levels are elevated, canvasbacks apparently reduce feeding and lose an average of 200 g body mass and 105 g fat (R. M. Pace, Natl. Biol. Serv., Baton Rouge, La., unpubl. data). Body mass and fat levels of canvasbacks at Catahoula Lake increase throughout winter (Hohman 1993), so risks to survival associated with Pb ingestion probably are greatest in November when immatures are leanest.

Whereas birds may survive Pb exposure in other months, reduced fat may affect timing and performance of subsequent annual cycle events. For example, if variation in fat levels regulates population ingress and egress at migratory stopover sites as suggested by Serie and Sharp (1989), then onset of spring migration may be delayed in Pb-exposed birds compared with unexposed birds. Reproductive performance of canvasbacks also may be affected by exposure to Pb in winter, if migration chronology is delayed in Pb-exposed individuals and time of arrival on spring staging and breeding areas (i.e., sites where birds initiate courtship and pair-bond formation [Weller 1965]) influences reproductive success (cf, Nichols and Haramis 1980*b*).

MANAGEMENT IMPLICATIONS

In spite of the ban on use of Pb shot by waterfowl hunters in the United States in 1991, ingestion of Pb shot deposited in wetlands before implementation of the ban remains a problem at some sites. Lead exposure in waterfowl should be monitored every 5 years (Havera et al. 1992). We further recommend that managers give priority to reducing Pb shot availability at important waterfowl concentration areas that are known to be contaminated with Pb. Manipulations of water levels to discourage bird use of contaminated areas may be only partially effective. For example, increasing water levels in contaminated areas may reduce their use by dabbling ducks but would have little effect on use by diving ducks. Establishment of sanctuaries with adequate feeding and resting areas and timing of flooding to reduce use during periods of the annual cycle when birds are lean may serve to lower mortality associated with Pb exposure in some species, but managers should strive to eliminate Pb from sediments where waterfowl foods occur. Techniques available to accomplish this objective (e.g., plowing; Fredrickson et al. 1977, Peters and Afton 1993) may require further investigation.

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ANNUAL HOME RANGES AND SPACING PATTERNS OF CAPERCAILLIE IN CENTRAL EUROPE

ILSE STORCH, Munich Wildlife Society, Linderhof 2, D-82488 Ettal, Germany

Abstract: The capercaillie (*Tetrao urogallus*) is endangered in Central Europe; knowledge of its spatial requirements is vague but important for conservation. I radiotracked 40 capercaillie during 1988–92 in the Bavarian Alps, Germany, to study annual range use patterns and to identify habitat needs for capercaillie conservation. Annual home ranges of females (n = 7) and males (n = 19) were not different in size (P = 0.56), diameter (P = 0.41), or vegetation (P > 0.15). Home range size varied between 132 and 1,207 ha, and averaged 550 ha (SE = 52 ha). Home range size was inversely related to availability of bilberry (*Vaccinium myrtillus*) (P < 0.001) and late stages of forest succession (P < 0.01) within the home range. Both sexes tended to occupy the same annual and seasonal home ranges in consecutive years. None of 7 females and 10 of 20 males used distinct, nonoverlapping midwinter and midsummer home ranges. Throughout the year, distances of females from the leks they attended in spring averaged 1.3 km (SE = 0.1 km). In winter and spring, males aggregated within a 1-km radius of the lek, but dispersed within a 3–4-km radius during summer. Males returned to leks between August and December. Timing of movements from the lek to the summer range was age related (P < 0.001), and >5-year-old males were the last to leave. Movements of males to summer ranges could not be explained by food sources and may be related to predator avoidance. In the course of a year, birds of 1 lek may use a 30–50-km^2 area. Therefore, maintaining leks and habitat within 3–4 km of the lek center should be emphasized in capercaillie conservation.

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The capercaillie inhabits late successional stages of Palaearctic boreal and montane forests. Open forest structure, conifers for winter food, and bilberry for summer food and cover are considered key elements of capercaillie habitat (Klaus et al. 1989, Rolstad and Wegge 1989, Picozzi et al. 1992, Storch 1994*a*). Since the 1960s, many Central European capercaillie populations have disappeared, and it has become an endangered species. In Germany, shooting of capercaillie has been banned since the 1970s, but continued population declines indicate habitat deterioration is causing the declines. In Central Europe, capercaillie conservation efforts have emphasized microhabitat features at the forest stand level, particularly at leks (Popp 1974, Rodenwald 1974, Stein 1974, Zeimentz 1974, Weiss 1988). However, Scan-