



ANTHELMINTICS INCREASE SURVIVAL OF AMERICAN COOT (*FULICA AMERICANA*) CHICKS

COURTNEY L. AMUNDSON¹ AND TODD W. ARNOLD

Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, St. Paul, Minnesota 55108, USA

ABSTRACT.—Helminthic parasites occur at high frequencies in waterbirds, but little is known about their effects on host population dynamics. In 2004–2005, we examined the effect of helminthic parasites on fledging success of semiprecocial American Coot (*Fulica americana*) chicks by experimentally dosing day-old chicks with the anthelmintic drug fenbendazole (treatments) or sterile water (controls) and measuring their survival to 40 days of age using mark–resighting analyses. In 2005, we also provided anthelmintic (treatment) or plain (control) supplemental food to incubating adults to determine whether chick survival was further influenced by parasite burdens of parents. Treated offspring had approximately half as many helminthic parasites as untreated offspring, but we could not demonstrate a reduction in parasite burdens among treated adults. Chicks that received fenbendazole in 2004 had 0.510 (85% confidence interval [CI]: 0.447–0.588) cumulative survival to 40 days of age, versus 0.387 (85% CI: 0.305–0.462) survival in untreated chicks. In 2005, offspring survival to 40 days posthatch was an additive function of both offspring and parental treatment, with survival averaging 0.578 (85% CI: 0.502–0.654) when both parents and chicks were treated, 0.461 (85% CI: 0.381–0.544) when only chicks were treated, 0.452 (85% CI: 0.375–0.533) when only adults were treated, and 0.334 (85% CI: 0.254–0.424) when neither was treated with fenbendazole. Our results provide compelling evidence that treatment with anthelmintic drugs increased fledging success and suggest that parasite burdens have important consequences for offspring survival in American Coots. Received 31 August 2009, accepted 6 January 2010.

Key words: American Coots, anthelmintics, fledging success, *Fulica americana*, helminths, Manitoba, parasites, survival.

Los Antihelmínticos Aumentan la Supervivencia de Polluelos de *Fulica americana*

RESUMEN.—Los parásitos helmínticos se encuentran con alta frecuencia en las aves acuáticas, pero se sabe poco acerca de sus efectos sobre la dinámica poblacional de sus hospederos. En 2004–2005, examinamos el efecto de parásitos helmínticos sobre el éxito de emplumamiento de polluelos de *Fulica americana*, una especie seminidífuga. Aplicamos dosis de la droga antihelmíntica fenbendazol (tratamientos) o de agua estéril (controles) a polluelos de un día de edad y medimos su supervivencia hasta los 40 días de vida, utilizando un análisis de marcado y re-avistamiento. En 2005, también proporcionamos alimento con adición de antihelmíntico (tratamiento) y sin adición (control) a los adultos que se encontraban incubando para determinar si la supervivencia de los polluelos era también influenciada por la carga parasitaria de los padres. La progenie tratada tuvo aproximadamente la mitad de parásitos helmínticos que la no tratada, pero no pudimos demostrar una reducción de la carga parasitaria en los adultos tratados. Los polluelos que recibieron la droga fenbendazol en 2004 tuvieron una supervivencia acumulativa hasta los 40 días de vida de 0.510 (intervalo de confianza del 85% [IC]: 0.447–0.588), versus una supervivencia de 0.387 (IC: 0.305–0.462) en los polluelos no tratados. En 2005, la supervivencia de la progenie hasta 40 días desde la eclosión fue una función aditiva del tratamiento en la progenie y en los adultos, con una supervivencia de 0.578 en promedio (IC: 0.502–0.654) cuando los dos padres y los polluelos fueron tratados, de 0.461 (IC: 0.381–0.544) cuando sólo los polluelos fueron tratados, de 0.452 (85% IC: 0.375–0.533) cuando sólo los adultos fueron tratados y de 0.334 (85% IC: 0.254–0.424) cuando ninguno de los dos fue tratado con fenbendazol. Nuestros resultados brindan evidencia substancial de que el tratamiento con drogas antihelmínticas aumenta el éxito de emplumamiento y sugieren que las cargas parasitarias tienen consecuencias importantes para la supervivencia de la progenie de *F. americana*.

PARASITES HAVE THE potential to reduce host fitness by exploiting limited resources that could otherwise be used for growth, survival, or reproduction (Møller and Erritzøe 2002). Helminths are primarily gastrointestinal parasites. They include trematodes (flukes), cestodes (tapeworms), nematodes (roundworms), and

acanthocephalans (thorny-headed worms) (Clayton and Moore 1997). Helminths can cause anorexia, disrupt the motility and secretions of the gastrointestinal tract, and damage the walls of the latter (Chowdhury and Tada 1994). Reduced food intake in combination with the increased metabolic needs of parasitized

¹E-mail: amun0113@umn.edu

animals may lead to decreased body condition and further suppression of the host's natural defenses against parasites (Chowdhury and Tada 1994). Aquatic birds usually acquire helminths by ingesting infected invertebrates, especially snails (Cole and Friend 1999). American Coots (*Fulica americana*; hereafter "coots") harbor a wide variety of helminthic parasites (Roudabush 1942, Colbo 1965, Kinsella 1973, Eley 1976, McLaughlin 1986), and immature coots are especially vulnerable to infection by *Cyclocoelum mutabile* (McKindsey et al. 1994).

Historically, research in avian parasitology focused primarily on the presence and species composition of parasites (LaPage 1962, Kocan et al. 1979), but recent experiments using anthelmintics (broad-spectrum drugs that kill many species of helminths) have begun to focus on the fitness consequences of parasite burdens (Hudson et al. 1992, Møller et al. 1999, Navarro et al. 2004). Hanssen et al. (2003) administered anthelmintics to adult female Common Eiders (*Somateria mollissima*) in northern Norway over a 2-year period and found that body condition was unaffected, but return rates (a proxy for survival) were higher for unsuccessful breeders. Newborn and Foster (2002) treated wild Red Grouse (*Lagopus lagopus scoticus*) with anthelmintic grit and found that treated adults had 34% fewer worms than those that received plain grit. Medicated grit did not significantly affect clutch size, hatching success, or adult survival, but it resulted in higher offspring survival, presumably because treated adults were in better condition and provided better care to their offspring. Juvenile Ross's Geese (*Chen rossii*) treated with anthelmintics had greater first-year survival than controls, although results were confounded with body condition (Slattery and Alisauskas 2002). However, newly hatched Eurasian Oystercatcher (*Haematopus ostralegus*) chicks treated with a combination of levamisole, oxyelozanide, and ivermectin had lower survival than controls, possibly because of an immunosuppressive effect of these anthelmintics (Van Oers et al. 2002).

We investigated the effects of parasites on reproduction in coots by experimentally providing the anthelmintic drug fenbendazole to newly hatched chicks (2004–2005) and incubating adults (2005) and documenting the subsequent survival of chicks to 40 days of age. Coot chicks are semiprecocial and are critically dependent on their parents for food during the first few weeks of life (Desrochers and Ankney 1986, Driver 1988). We predicted that chicks dosed with fenbendazole would have lower parasite burdens and that this would enhance their ability to solicit food from parents and, thus, increase their survival compared with untreated control chicks. Alternatively, lower parasite burdens might increase the digestive efficiency of chicks, which could reduce their food requirements and, therefore, increase their survival. We further predicted that breeding adults that received fenbendazole would have lower parasite burdens and that this would enhance their ability to care for dependent offspring and, thus, improve the survival of their offspring compared with those of untreated parents.

METHODS

Study area.—We conducted our research at the Delta Waterfowl Research Station, located ~9 km southwest of Minnedosa, Manitoba (50°10'N, 99°47'W), during the 2004–2005 breeding seasons.

Minnedosa has a high density of 0.1–2.0 ha semipermanent and permanent wetlands that provide ideal nesting habitat for coots in all but extreme drought years (Kiel 1955, Arnold 1994, Reed 2000). Our study area included 16 (2004) and 31 (2005) different semipermanent and permanent wetlands with large central expanses of open water that were completely visible from the road.

Experimental design.—We conducted systematic overwater nest searches of the emergent vegetation, beginning on 20 May 2004 and on 5 May 2005 (the 2004 nesting season was delayed by two snowstorms in early May) and continuing weekly until the end of June. Most nests were found during laying, and initiation dates were estimated by back dating, assuming that 1 egg was laid per day (Arnold 1994). The first nest to hatch in each wetland was randomly assigned to one of four treatment groups: (1) full brood treated (treatment, T); (2) every other chick treated, starting with the first chick as a treatment (alternating, A₁); (3) every other chick treated, with the first chick as a control (alternating, A₂); or (4) no chicks treated (control, C). Subsequent nests on each pond were assigned to the next treatment group in a fixed rotation (T, A₁, A₂, C). Alternating treatment groups were created to determine whether survival was affected by within-brood competitive hierarchies (e.g., Lyon et al. 1994), but there was no compelling evidence that survival varied in relation to the treatment regime of broodmates (Amundson 2007) and so we simply focused on whether an individual chick was a treatment or a control. Experimental coot nests were visited daily throughout the estimated hatching period, and any pipped eggs were collected and individually marked with their nest and egg numbers written with a thin black permanent marker at one end of each egg. Eggs were placed in an artificial incubator and allowed to hatch in captivity.

We used fenbendazole (methyl N-[6-phenylsulfanyl-1H-benzimidazol-2-yl]carbamate) as a prophylactic to delay helminth infestations in hatchling coots. Fenbendazole has several potential advantages over alternative anthelmintics: (1) it is safe at dosages more than 100× clinical doses; (2) it is broad spectrum and effective against eggs, adults, and larval stages of several species of helminths; (3) it is palatable and can be administered in the diet with no loss of appetite; and (4) even low doses can be effective (Adams 2001, Newborn and Foster 2002). Newly hatched chicks were weighed (± 0.1 g) and individually color-marked with nape-tags consisting of two plastic Perler beads (see Acknowledgments) on a brass safety-pin (Reed 2000). Chicks were treated orally with 0.05 cc of fenbendazole (diluted to 20 mg mL⁻¹) at a dosage rate of 50 mg kg⁻¹ body mass. Control chicks were given an equivalent dose of sterile water. Treatments and controls were administered using a 1-cc sterile syringe with a modified extended tip to allow the syringe to reach past the glottis to ensure that the liquid was not aspirated. Marked chicks were returned to their nest bowls within 12 h of hatching (usually within 6 h).

In 2005, the first clutch completed was randomly assigned as a parental treatment or control group and all subsequent wetlands were alternated as treatments or controls. Parental treatment was assigned by wetland rather than by nest to prevent neighboring adults from utilizing feeding platforms in an adjacent territory (Arnold 1994). After clutch completion, a 60 × 60 cm floating platform was placed approximately 10–15 m from each nest. Platforms were supplied with 2 kg of cracked corn that was either treated (coated with 60 mL vegetable oil mixed with 11.4 g of fenbendazole

powder) or untreated (coated with 60 mL vegetable oil only). Feeding platforms were removed after the first chick hatched to prevent parents from feeding chicks food from the platforms. Mean availability of feeding platforms to adults was 14 days (range: 8–20 days; $n = 55$). Coots were observed feeding from the platforms on several occasions (see Arnold 1994), although few platforms had been emptied before food replacement occurred on day 7.

Re-observations of marked chicks began 5 days after the first chick hatched and continued until 44 days after all chicks had hatched. We subdivided the sampling effort into five age-specific periods: 1–10 days, 11–20 days, 21–30 days, 31–40 days, and 41–50 days old. Chick observations were conducted using a 15–60× spotting scope from a parked vehicle and lasted 1 h or until all marked chicks were identified. Broods were observed on a weekly rotation in 2004 and every 3 days in 2005, with successive observation periods alternating between morning and afternoon. Nests where no chicks were seen were revisited every other day (every 3 days in 2005) until chicks were seen, determined to have moved to an adjacent wetland, or presumed to have died.

Statistical analyses.—Mark-resighting data were analyzed with Cormack-Jolly-Seber open population models using Program MARK (White and Burnham 1999). Apparent survival (ϕ_i) is the probability that an individual alive at age i survives until age $i + 1$ and does not permanently emigrate from the study population. Because we were working on prefledged territorial waterbirds inhabiting small wetlands, we believe that emigration was negligible, and our estimates therefore represent true survival. Resighting rate (p_i) is the probability that an individual that is alive at age i is seen on that occasion. Controlling for sightability is important in coots because chicks spend considerable time concealed in emergent vegetation and broodmates are rarely seen all together (Reed 2000). Encounter histories for each chick were coded as follows to comprise six capture occasions: 0 = release day (age 0 days), 1 = 10 days, 2 = 20 days, 3 = 30 days, 4 = 40 days, and 5 = 50 days old. If a chick was seen at any time between two occasions it was coded as observed (1) on the latter occasion, whereas chicks that were not seen during the interval were coded as not observed (0); that is, a chick released on day 0 and observed 7, 25, and 43 days later would receive a capture history of 110101. Data for 2004 were coded using two attribute groups (chicks treated vs. chicks untreated), whereas data for 2005 were coded using four attribute groups (\pm chick treatment, \pm adult treatment; treatment effects are denoted as “chick” and “adult” in model notation). Because treatment protocols differed between years, data from each year were analyzed separately.

The most general model that allowed survival and resighting rates to vary independently among all combinations of treatment groups and age classes (i.e., 2005 Model $\phi_{(1,2,3,4,5)} \text{Chick}^* \text{Adult}^* p_{(1,2,3,4,5)} \text{Chick}^* \text{Adult}^*$) was used to examine overdispersion in the data (Burnham and Anderson 2002). We conducted a bootstrap goodness-of-fit test in MARK to estimate a variance inflation factor (\hat{c}) by dividing the observed deviance of the most general model by the mean deviance from 1,000 bootstrap simulations (White et al. 2001). Model-fitting decisions were based on Akaike’s information criterion corrected for sample size and overdispersion (QAIC_c; Burnham and Anderson 2002). The best-supported model was determined by the lowest QAIC_c value and highest Akaike weight (w_i ; Burnham and Anderson 2002).

To facilitate the most powerful exploration of treatment effects on survival, we first fit reduced-parameter models of resighting rates and age-related variation in survival rates (Lebreton et al. 1992). Survival and resighting rates were first treated as either age-specific (i.e., separate estimates for each age class; $\phi_{(1,2,3,4,5)}$, $p_{(1,2,3,4,5)}$) or age-invariant (i.e., constant across all age intervals; $\phi_{(1-5)}$, $p_{(1-5)}$), and then hybrid models allowing pooling of adjacent intervals were examined (e.g., $\phi_{(1,2-5)}$ implies pooled estimates of ϕ for ages 10–50 days). Mortality is usually highest when offspring are young but often reaches a stable plateau among older age classes (Chouinard and Arnold 2007, Mehl and Alisauskas 2007). We did not expect anthelmintic treatment to influence resighting rates, so we also evaluated models that treated resighting rates as equivalent between treatment groups.

After modeling age-specific variation in resighting and survival rates and treatment effects on resighting rates, we evaluated treatment effects on survival using the best-supported model from the previous step. In addition to testing for survival differences among treatment groups (e.g., ϕ_{Chick} , $\phi_{\text{Chick}^* \text{Adult}^*}$), we also evaluated link functions that considered treatment effects as additive rather than factorial (i.e., logit parallelism; Lebreton et al. 1992). For example, given five age-specific survival parameters ($\phi_{(1,2,3,4,5)}$), evaluation of an independent treatment effect would require five additional parameters ($\phi_{(1,2,3,4,5)} \text{Chick}^*$ allowing for independent treatment effects at each age interval), whereas an additive model would require only one additional parameter and treatment effects would be constrained to be of similar magnitude across all five age intervals ($\phi_{(1,2,3,4,5)} + \text{Chick}^*$). In addition to treatment-by-age additivity, we allowed chick versus adult treatments in 2005 to behave in a potentially additive fashion ($\phi_{\text{Chick} + \text{Adult}}$). Additive effects were modeled using logit link functions and design matrix constraints in MARK (Cooch and White 2010).

Cumulative survival to 40 days of age was estimated as the product of individual survival estimates from each 10-day interval (e.g., $\phi_1 \cdot \phi_2 \cdot \phi_3 \cdot \phi_4$). We report cumulative survival estimates with 85% confidence intervals (CI) derived from 10,000 bootstraps of real parameter estimates in MARK; we used 85% CI because they are more compatible with AIC-based model selection (Arnold 2010). Fledging rates for each treatment group and year were calculated by multiplying mean initial brood size by cumulative survival to 40 days of age.

RESULTS

2004 experiment.—We collected survivorship data from 322 coot chicks from 38 nests in 2004. Only 13 chicks were resighted during the age interval of 41–50 days, compared with 90–121 chicks in each of the prior four age intervals, so we excluded the final sampling occasion from our analysis in 2004. The bootstrap goodness-of-fit test on model $\phi_{(1,2,3,4)} \text{Chick}^* p_{(1,2,3,4)} \text{Chick}^*$ revealed little evidence of overdispersion ($\hat{c} = 1.16$), but we nevertheless included this slight variance-correction factor for subsequent modeling. The best-supported model for the effects of age on resighting probability ($p_{(1,2,3,4)}$) recognized all four intervals as unique ($p_1 = 0.481$, $p_2 = 0.620$, $p_3 = 0.762$, $p_4 = 0.612$), whereas ages 10–40 days could be pooled for estimating survival ($\phi_{(1,2-4)}$); this latter constraint allowed us to estimate survival to 40 days of age despite deletion of the last resighting interval. The best overall model ($\phi_{(1,2-4)} + \text{Chick}^* p_{(1,2,3,4)}$)

TABLE 1. Models of survival (ϕ) and resighting rate (p) in American Coots (southwestern Manitoba, 2004) to 40 days of age in relation to chick age (1: 0–10 days, 2: 10–20 days, etc.) and fenbendazole treatment of chicks (Chick). Models are ranked by differences in quasi-AIC (ΔQAIC_c) and relative model weights (w_i). K is the number of estimable parameters, and QDev is $-2\log L/\hat{c}$, where $\hat{c} = 1.16$.

Model ^a	ΔQAIC_c	w_i	K	QDev
$\phi_{(1,2-4)+\text{Chick}}, p_{(1,2,3,4)}$	0.00	0.33	7	1,173.76
$\phi_{(1,2-4)}, p_{(1,2,3,4)}$	1.33	0.17	6	1,177.13
$\phi_{(1,2-4)*\text{Chick}}, p_{(1,2,3,4)}$	1.87	0.13	8	1,173.58
$\phi_{(1,2-4)*\text{Chick}}, p_{(1,2,3,4)+\text{Chick}}$	2.90	0.08	9	1,172.55
$\phi_{(1,2,3,4)}, p_{(1,2,3,4)}$	3.37	0.06	7	1,177.13
$\phi_{(1,2-4)*\text{Chick}}, p_{(1,2,3,4)*\text{Chick}}$	5.24	0.02	12	1,168.68
$\phi_{(1,2,3,4)*\text{Chick}}, p_{(1,2,3,4)*\text{Chick}}$	10.70	0.00	15	1,167.87

^a QAIC_c for best-supported model = 1,187.934.

TABLE 2. Models of chick survival (ϕ) and resighting probabilities (p) in American Coots (southwestern Manitoba, 2005) to 40 days of age in relation to chick age (1: 0–10 days, 2: 10–20 days, etc.) and fenbendazole treatment of chicks and adults. Models are ranked by differences in quasi-AIC (ΔQAIC_c) and relative model weights (w_i). K is the number of estimable parameters, and QDev is $-2\log L/\hat{c}$, where $\hat{c} = 1.66$.

Model ^a	ΔQAIC_c	w_i	K	QDev
$\phi_{(1,2-3,4)+\text{Chick}+\text{Adult}}, p_{(1-5)}$	0	0.26	7	1,037.86
$\phi_{(1,2-3,4)+\text{Chick}}, p_{(1-5)}$	0.76	0.18	6	1,040.66
$\phi_{(1,2-3,4,5)+\text{Adult}}, p_{(1-5)}$	1.21	0.14	6	1,041.11
$\phi_{(1,2-3,4,5)}, p_{(1-5)}$	1.46	0.13	5	1,043.4
$\phi_{(1,2-3,4,5)+\text{Adult}*\text{Chick}}, p_{(1-5)}$	1.80	0.11	8	1,037.62
$\phi_{(1,2-3,4,5)*\text{Adult}}, p_{(1-5)}$	4.63	0.03	9	1,038.41
$\phi_{(1,2-3,4,5)*\text{Chick}}, p_{(1-5)}$	6.13	0.01	9	1,039.9
$\phi_{(1,2-3,4,5)*\text{Adult}*\text{Chick}}, p_{(1-5)}$	15.51	0	17	1,032.71

^a QAIC_c for best-supported model = 1,052.01.

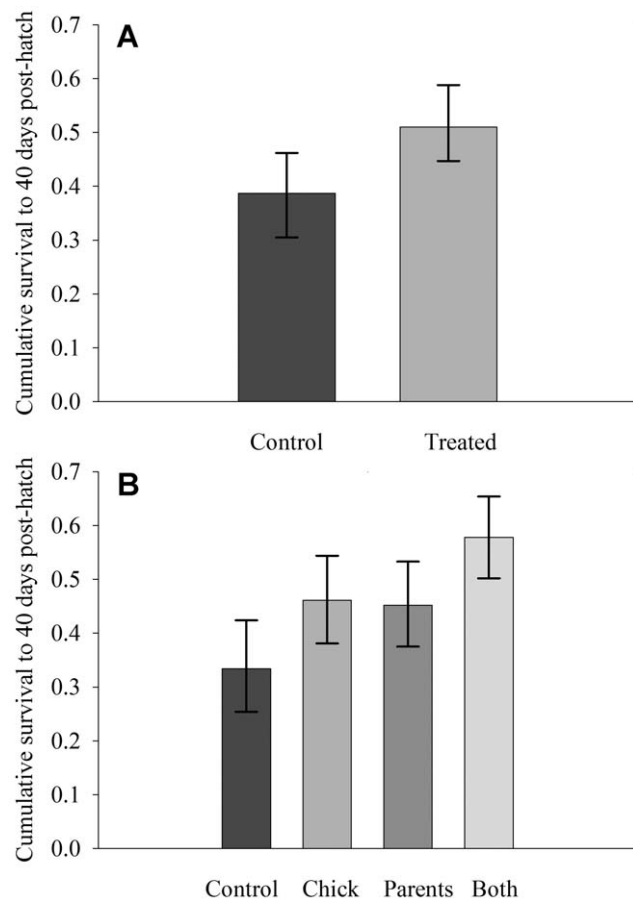


FIG. 1. Effect of fenbendazole on 40-day cumulative survival (\pm 85% confidence intervals) of coot chicks in southwestern Manitoba. Estimates are from the best-approximating model in Tables 1 and 2. In 2004, only chicks were treated, whereas in 2005 we utilized a fully factorial design whereby both chicks and parents were treated.

recognized an additive effect of fenbendazole treatment on chick survival over all age classes ($\beta = 0.412$, 85% CI: 0.090–0.734), and this model had twice as much support as a simpler model that recognized no treatment effect (Table 1). Cumulative survival to 40 days of age was higher for chicks that were treated with fenbendazole (0.510, 85% CI: 0.447–0.588) than for untreated control chicks (0.387, 85% CI: 0.305–0.462; Fig. 1). On the basis of an average initial brood size of 7.88 chicks, parents of treated chicks would have fledged 4.03 young (85% CI: 3.52–4.63), whereas parents of control chicks would have fledged an average of 3.06 young (85% CI: 2.40–3.64).

2005 experiment.—We collected survivorship data from 340 chicks from 40 broods in 2005. The bootstrap goodness-of-fit test on the full model ($\phi_{(1,2,3,4,5)*\text{Chick}*\text{Adult}}, p_{(1,2,3,4,5)*\text{Chick}*\text{Adult}}$) revealed modest evidence of overdispersion ($\hat{c} = 1.66$). The best-fitting model for resighting probability recognized constant sightability across all treatment groups and age classes (Table 2; $p_{(1-5)} = 0.567$, 85% CI: 0.531–0.601). Estimated survival probabilities for ages 10–20 and 20–30 days were often 100%, so we pooled these two intervals to help minimize the number of inestimable parameters. Cumulative QAIC_c weights (Σw_i) were 0.67 for models incorporating chick treatment effects, 0.63 for models incorporating adult treatment effects, 0.45 for models incorporating both, and 0.15 for models incorporating neither (Table 2). The best-fitting model ($\phi_{(1,2-3,4,5)+\text{Chick}+\text{Adult}}, p_{(1-5)}$) recognized additive effects of fenbendazole treatment on both chicks ($\beta = 0.444$, 85% CI: 0.089–0.800) and adults ($\beta = 0.413$, 85% CI: 0.058–0.769) over all age classes. Cumulative survival to 40 days of age was highest when both chicks and adults were treated with fenbendazole (0.578, 85% CI: 0.502–0.654; Fig. 1). If either the chicks or the adults had been treated, survival was intermediate (chicks treated: 0.461, 85% CI: 0.381–0.544; adults treated: 0.452, 85% CI: 0.375–0.533). And if neither chicks nor adults received anthelmintics, cumulative survival was only 0.334 (85% CI: 0.254–0.424). On the basis of an average initial brood size of 8.90, estimated fledging rates were highest for treated adults with treated chicks (5.14, 85% CI: 4.47–8.82), followed by control adults with treated chicks (4.10, 85% CI: 3.39–4.84) and treated parents with control chicks (4.02, 85% CI: 3.34–4.74);

the lowest rates were for control parents with control chicks (2.97, 85% CI: 2.26–3.77).

DISCUSSION

Anthelmintic treatment resulted in a significant 54% reduction in parasite burdens among immature coots ($P = 0.04$) but had no discernible effect ($P = 0.48$) on parasite burdens in adults (Amundson 2007). Nevertheless, anthelmintic treatment of both hatchlings and adults led to increased offspring survival. Broods that were fully treated with fenbendazole fledged from 1.0 to 1.1 more chicks per brood than untreated broods in 2004 and 2005, representing 28–38% increases in mean fledging success. Treating parents with fenbendazole in 2005 increased fledging success by an additional 1.0 chicks per brood. For broods in 2005 in which both parents and chicks were treated, fledging success increased by 73% over what we observed in untreated broods.

Coot chicks are fed mainly aquatic invertebrates early in life (Driver 1988), so parasite transmission could occur almost immediately after hatch. We suspected that by reducing parasite burdens early in life, a large part of the survival benefit would be observed at later ages when control chicks began suffering the effects of more advanced parasitic infections (i.e., from adult worms). However, survival advantages were observed throughout the first 40 days of life, which suggests that reduction of parasites resulted in an immediate benefit to treated chicks. Møller and Saino (2004) recently reviewed the role of the immune system in bird survival and found that survivorship in young birds was positively correlated with the ability to mount a strong immune response, as measured by T-lymphocyte cell-mediated immune response. Although we did not measure immune-response functions or parasite burdens in very young chicks, we suspect that reducing parasites in younger chicks may have improved their survival prospects by alleviating parasite-derived taxation of their immune systems (Møller and Saino 2004, Amat et al. 2007). Tschirren and Richner (2006) found that nestling Great Tits (*Parus major*) with experimentally bolstered immune systems grew slower than unstimulated chicks, which implies a tradeoff between investments in growth and immune response. Additionally, chicks with boosted immune systems grew faster than control chicks when both were experimentally infected with ectoparasites, which demonstrated the benefit of mounting an immune response to parasite defense and the cost of parasites to growth rates in young birds.

Coots hatch more chicks than they can typically fledge, and almost all broods experience some level of brood reduction through selective feeding of specific chicks (Lyon 1993, Lyon et al. 1994; T. Arnold unpubl. data). Survival is highest among chicks that hatch first (Lyon 1993), have brighter plumage (Lyon et al. 1994), or hatch from larger eggs (T. Arnold unpubl. data), and parents seem to exert almost complete control over which chicks are fed (Lyon et al. 1994). Parasite burdens (or some other aspect of anthelmintic treatment) may have influenced feeding decisions by parents, which may have exacerbated differences in relative fitness among offspring. In addition to colorful head plumage, coot chicks also shunt blood into their bare napes when begging (Lyon et al. 1994; see also Nuechterlein 1985), and treatment with anthelmintics may have allowed chicks to better advertise their health to parents. Because coot chicks compete with their broodmates for

parental resources, an increase in health or condition of individual chicks should allow them to compete more effectively against their broodmates and therefore increase their relative prospects of survival (Lyon et al. 1994). Chicks in better condition may be better able to beg for food, survive short periods of parental neglect, and thereby alleviate the negative effects of hatching asynchronously (Lyon et al. 1994). In both years, there was modest support for models that recognized higher survival of fenbendazole-treated chicks versus untreated chicks within the same broods (fig. 2 in Amundson 2007), although these models fit less well than models that simply recognized an overall treatment effect, regardless of brood composition. Lyon et al. (1994) found that plumage manipulation affected chick survival only when chicks competed against broodmates with more colorful plumage, which suggests that coot parents assess and discriminate among offspring. Similarly, Christe et al. (1996) found that parents were more likely to engage in differential feeding among Great Tit broods where ectoparasite burdens had been experimentally increased. Although we did not measure begging rates or differential feeding of treated versus untreated chicks, our reduction of parasites in coot chicks may have improved their ability to communicate their enhanced survival prospects to their parents, and this might be a productive avenue for future research.

We also found an effect of treating parents with fenbendazole—treated parents fledged 25–35% more chicks than untreated parents—and this effect was additive to that observed from treating chicks alone. This is consistent with previous studies that demonstrated enhanced fledging success among adult Red Grouse and Ring-necked Pheasants (*Phasianus colchicus*) that received anthelmintic-treated food (Newborn and Foster 2002, Draycott et al. 2006). Reed et al. (2008) found that anthelmintic treatment of adult European Shags (*Phalacrocorax aristotelis*) led to increased survival of male offspring, and the authors concluded that a decrease in parasite burdens led to an increase in maternal investment in young, specifically the more energetically expensive male offspring.

We have shown that treatment of both adult and hatchling coots with anthelmintics led to substantial increases in offspring survival; however, the mechanism for this advantage remains unclear and may involve alterations in relative parental investment as opposed to direct effects of helminthic parasites on chick survival. Future studies that examine investment decisions of parents in response to among-brood variation in parasite infestation may prove insightful (Christe et al. 1996), as would studies that identify the causal link between parasite infections and fledging success (Amat et al. 2007).

ACKNOWLEDGMENTS

We thank K. Wlock, A. Olivarez, and E. Widi for help in data collection and A. Pagano for parasite identification and comments on earlier drafts of the manuscript. T. Quirk, J. Pitt, D. Coulton, and L. Reichart were invaluable both in coot collection and field logistics. We thank Delta Waterfowl Foundation for providing funding for this research as well as the use of the Minnedosa Field Station. Additional funding was provided by the F. M. Chapman Memorial Fund of the American Museum of Natural History and the Dayton-Wilkie Natural History Fund of the Bell Museum of

Natural History. Perler beads are available at www.perlerbeads.com. Special thanks to Dick MacDonald (1936–2007) for volunteering his time to make the Minnedosa Field Station an amazing place to conduct research. We could not have done it without him.

LITERATURE CITED

- ADAMS, H. R., Ed. 2001. Veterinary Pharmacology and Therapeutics, 8th ed. Iowa State University Press, Ames.
- AMAT, J. A., E. AGUILERA, AND G. H. VISSER. 2007. Energetic and developmental costs of mounting an immune response in Greenfinches (*Carduelis chloris*). *Ecological Research* 22:282–287.
- AMUNDSON, C. L. 2007. The impacts of helminthic parasites on survival of American Coot (*Fulica americana*) chicks. M.S. thesis, University of Minnesota, St. Paul.
- ARNOLD, T. W. 1994. Effects of supplemental food on egg production in American Coots. *Auk* 111:337–350.
- ARNOLD, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management* 74: in press.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd ed. Springer-Verlag, New York.
- CHOUINARD, M. P., JR., AND T. W. ARNOLD. 2007. Survival and habitat use of Mallard (*Anas platyrhynchos*) broods in the San Joaquin Valley, California. *Auk* 124:1305–1316.
- CHOWDHURY, N., AND I. TADA. 1994. Helminthology. Narosa Publishing House, New Delhi, India.
- CHRISTE, P., H. RICHNER, AND A. OPPLIGER. 1996. Begging, food provisioning, and nestling competition in Great Tit broods infested with ectoparasites. *Behavioral Ecology* 7:127–131.
- CLAYTON, D. H., AND J. MOORE, Eds. 1997. Host-Parasite Evolution: General Principles and Avian Models. Oxford University Press, Oxford, United Kingdom.
- COLBO, M. H. 1965. Taxonomy and ecology of the helminths of the American Coot in Alberta. Ph.D. dissertation, University of Alberta, Edmonton.
- COLE, R. A., AND M. FRIEND. 1999. Section 5: Parasitic diseases. Pages 193–249 in *Field Manual of Wildlife Diseases: General Field Procedures and Diseases of Birds* (M. Friend and J. C. Fransen, Eds.). U.S. Geological Survey Biological Resources Division, Denver, Colorado. [Online.] Available at purl.access.gpo.gov/GPO/LPS69538.
- COOCH, E., AND G. C. WHITE. 2010. Program MARK: "A Gentle Introduction," 9th ed. [Online.] Available at www.phidot.org/software/mark/docs/book.
- DESROCHERS, B. S., AND C. D. ANKNEY. 1986. Effect of brood size and age on the feeding behavior of adult and juvenile American Coots (*Fulica americana*). *Canadian Journal of Zoology* 64:1400–1406.
- DRAYCOTT, R. A. H., M. I. A. WOODBURN, D. E. LING, AND R. B. SAGE. 2006. The effect of an indirect anthelmintic treatment on parasites and breeding success of free-living pheasants *Phasianus colchicus*. *Journal of Helminthology* 80:409–415.
- DRIVER, E. A. 1988. Diet and behaviour of young American Coots. *Wildfowl* 39:34–42.
- ELEY, T. J. 1976. Helminth parasites in American Coots from the lower Colorado River. *California Fish and Game* 62:156–157.
- HANSSEN, S. A., I. FOLSTAD, K. E. ERIKSTAD, AND A. OKSANEN. 2003. Costs of parasites in Common Eiders: Effects of antiparasite treatment. *Oikos* 100:105–111.
- HUDSON, P. J., D. NEWBORN, AND A. P. DOBSON. 1992. Regulation and stability of a free-living host–parasite system: *Trichostrongylus tenuis* in Red Grouse. I. Monitoring and parasite reduction experiments. *Journal of Animal Ecology* 61:477–486.
- KIEL, W. H., JR. 1955. Nesting studies of the coot in southwestern Manitoba. *Journal of Wildlife Management* 19:189–198.
- KINSELLA, J. M. 1973. Helminth parasites of the American Coot *Fulica americana americana* on its winter range in Florida. *Proceedings of the Helminthological Society of Washington* 40:240–242.
- KOCAN, A. A., M. G. SHAW, AND P. M. MORGAN. 1979. Some parasitic and infectious diseases in waterfowl in Oklahoma. *Journal of Wildlife Diseases* 15:137–141.
- LAPAGE, G. 1962. A list of the parasitic protozoa, helminths and arthropoda recorded from species of the family Anatidae (ducks, geese, and swans). *Parasitology* 103:67.
- LEBRETON, J.-D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs* 62:67–118.
- LYON, B. E. 1993. Conspecific brood parasitism as a flexible female reproductive tactic in American Coots. *Animal Behaviour* 46:911–928.
- LYON, B. E., J. M. EADIE, AND L. D. HAMILTON. 1994. Parental choice selects for ornamental plumage in American Coot chicks. *Nature* 371:204–243.
- MCKINDSEY, C. W., J. K. GORING, AND J. D. MCLAUGHLIN. 1994. In vivo and in vitro studies on the viability and the infectivity to coots, *Fulica americana* of *Cyclocoelum mutabile metacercariae* from three species of snails. *Canadian Journal of Zoology* 72:1186–1190.
- MCLAUGHLIN, J. D. 1986. The biology of *Cyclocoelum mutabile* (Trematoda) infections in American Coots. *Proceedings of the Helminthological Society of Washington* 53:177–181.
- MEHL, K. R., AND R. T. ALISAUSKAS. 2007. King Eider (*Somateria spectabilis*) brood ecology: Correlates of duckling survival. *Auk* 124:606–618.
- MØLLER, A. P., P. CHRISTE, AND E. LUX. 1999. Parasitism, host immune function, and sexual selection. *Quarterly Review of Biology* 74:3–20.
- MØLLER, A. P., AND J. ERRITZØE. 2002. Coevolution of host immune defence and parasite-induced mortality: Relative spleen size and mortality in altricial birds. *Oikos* 99:95–100.
- MØLLER, A. P., AND N. SAINO. 2004. Immune response and survival. *Oikos* 104:299–304.
- NAVARRO, C., F. DE LOPE, A. MARZAL, AND A. P. MØLLER. 2004. Predation risk, host immune response, and parasitism. *Behavioral Ecology* 15:629–635.
- NEWBORN, D., AND R. FOSTER. 2002. Control of parasite burdens in wild Red Grouse *Lagopus lagopus scoticus* through the indirect application of anthelmintics. *Journal of Applied Ecology* 39:909–914.
- NUECHTERLEIN, G. L. 1985. Experiments on the functions of the bare crown patch of downy Western Grebe chicks. *Canadian Journal of Zoology* 63:464–467.

- REED, T. E., F. DAUNT, M. E. HALL, R. A. PHILLIPS, S. WANLESS, AND E. J. A. CUNNINGHAM. 2008. Parasite treatment affects maternal investment in sons. *Science* 321:1681–1682.
- REED, W. R. 2000. Maternal effects in the American Coot: Consequences for offspring growth and survival. Ph.D. dissertation, Iowa State University, Ames.
- ROUDABUSH, R. K. 1942. Parasites of the American Coot (*Fulica americana*) in Iowa. *Iowa State College Journal of Science* 41:437–441.
- SLATTERY, S. M., AND R. T. ALISAUSKAS. 2002. Use of the Barker model in an experiment examining covariate effects on first-year survival in Ross's Geese (*Chen rossii*): A case study. *Journal of Applied Statistics* 29:497–508.
- TSCHIRREN, B., AND H. RICHNER. 2006. Parasites shape the optimal investment in immunity. *Proceedings of the Royal Society of London, Series B* 273:1773–1777.
- VAN OERS, K., D. HEG, AND S. L. D. QUENEC'H DU. 2002. Anthelmintic treatment negatively affects chick survival in the Eurasian Oystercatcher *Haematopus ostralegus*. *Ibis* 144:509–517.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46 (Supplement):S120–S138.
- WHITE, G. C., K. P. BURNHAM, AND D. R. ANDERSON. 2001. Advanced features of Program MARK. Pages 368–377 in *Wildlife, Land, and People: Priorities for the 21st Century* (R. Field, R. J. Warren, H. Okarma, and P. R. Sievert, Eds.). *Proceedings of the Second International Wildlife Management Congress*. Wildlife Society, Bethesda, Maryland.

Associate Editor: T. L. Shaffer