EFFECT OF CONSPECIFIC BROOD PARASITISM ON HOST FITNESS FOR TUFTED DUCK AND COMMON POCHARD

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ABSTRACT.—Brood parasitism occurs disproportionately in birds with precocial young and is particularly common in Anseriformes. In part, that pattern may result because precocial hosts, relative to altricial species, incur relatively few costs when caring for precocial eggs. Empirical data do not consistently support that hypothesis, and some parameters have not been adequately compared between parasitized and nonparasitized nests or females. We used a combination of experimentation (egg and duckling additions) and analysis of a larger observational data set to compare reproductive parameters, recruitment, and adult survival between parasitized and nonparasitized female Common Pochard (*Aythya ferina*) and Tufted Ducks (*A. fuligula*). Addition of three eggs to nests during the host's laying cycle had no effect on host clutch size, host egg hatch success, or nest success for either species. Nest success was not affected by parasitism intensity for pochards, but we did detect a small drop in nest success for Tufted Duck nests parasitized with >6 eggs. Recruitment probability did not differ between parasitized and nonparasitized nests for either species, and parasitism had no negative effect on adult survival. Between-year nest initiation dates were later for parasitized Tufted Ducks, although the biological consequences of that difference (3.8 days) seem negligible. Moderate levels of parasitism do not negatively affect hosts for these two species. *Received 27 September 2000, accepted 25 January 2001.*

PARENTAL CARE OFTEN ENTAILS a high cost to the parents; thus, it is not surprising that parasitic reproductive tactics have evolved that emancipate parasitic females from providing parental care (Hamilton and Orians 1965, Payne 1977). However, obligate brood parasitism is rare; facultative inter- and intraspecific parasitism is more common (Yom-Tov 1980, Rohwer and Freeman 1989, Sayler 1992). The success of parasitism will depend, in part, on how parasitism affects host reproductive success (Eadie et al. 1988, Rohwer and Freeman 1989). For altricial species, parasitism has been shown to reduce host reproductive success (reviewed in Rothstein 1990). In contrast, for precocial species, because parental care can be shared, brood parasitism may have no effect on host reproductive success (Rohwer and Freeman 1989). The difference in how parasitism affects altricial versus precocial host fitness may be responsible for conspecific brood parasitism being more common in precocial species (Roh-

wer and Freeman 1989, although see Sorenson 1992).

Among precocial species, conspecific brood parasitism has been most frequently studied in waterfowl (Rohwer and Freeman 1989, Sayler 1992). Those studies do not unanimously support the idea of no cost to host. Hosts may suffer lower nest success (McCamant and Bolen 1979, Haramis and Thompson 1985, Lank et al. 1990), clutch sizes (Andersson and Eriksson 1982), and hatching success (Amat 1985, Sorenson 1997). In contrast, others have suggested hosts benefit via increased offspring survival (Nudds 1980, Eadie and Lumsden 1985). Such variation has led some to question the use of the term *parasitism* (which presumes costs to hosts), at least in the absence of better data (Eadie et al. 1988).

For precocial birds, attempts to address the question of parasitism's effect on host reproduction have largely used observational methodologies (reviewed in Dugger 1996). Data from such studies can be difficult to interpret. For example, conspecific brood parasitism, clutch size, and nest success all commonly exhibit seasonal trends (Rohwer 1992, Sayler 1992, Dugger 1996), and many studies fail to control potential covariation in those trends.

Thus, it is difficult to ascertain whether smaller host clutch sizes and lower nest success were caused by parasitism, or result because parasitism was more common late in the host's breeding season when clutch size and nest success can be lower for other reasons (Amat 1987). Additional problems include failure to distinguish between host eggs and parasite eggs when estimating parameters such as clutch size, and failure to monitor nests during laying to identify origin of eggs found outside the nest bowl (Amat 1987, Eadie 1989, Dugger 1996). Although such data are useful for answering questions about parasitism's effect on population parameters, they likely bias attempts to understand parasitism's effect on individuals. A better way to obtain individual fitness data is to use study designs that actively manipulate the nest environment and subsequently measure the effect on host productivity (Reznick 1985). We use experimentation and correlative analyses to compare reproductive success and adult survival between nonparasitized and parasitized female Tufted Ducks (*Aythya fuligula*) and Common Pochards (*A. ferina*, hereafter called pochards).

METHODS

Study area.—Data were collected at Engure Marsh, Latvia (57°15′N, 23°07′E). Located along the western shore of the Gulf of Riga, which opens onto the eastern coast of the Baltic Sea, Engure Marsh is a 35 km², shallow, palustrine, persistent, emergent wetland. During the study, the distribution and coverage of the dominant emergent hydrophytes including common reed (*Phragmites australis*), cattail (*Typha* spp.), and alkali bulrush (*Scirpus lacustris*) approached 50:50 cover:water ratio. Both species nested on natural and artificial islands and floating mats of emergent vegetation. For a more detailed description of the study area see Blums et al. (1996).

Field procedures.—During summers of 1992–1993, nest searches were conducted every four to six days to locate nests during laying. Searches involved three to five people systematically walking all habitats in parallel transects. The distance between transects varied from 1.5 to 3.0 m as vegetation height and density varied. Nests found during laying with one, two, or three eggs were alternately assigned to either a treatment or control group for an egg-addition experiment. We used only nests found early in the female's laying cycle to assure that hosts would have time to respond to the manipulation (Kennedy 1991). Alternately assigning nests assured that both treatment and control nests were equally affected by po-

tential covariation between clutch size and initiation date.

Treatment nests received three conspecific eggs. Experimental eggs were collected from other nests around the marsh and were always day 0 incubation. In all but one instance, all eggs were added at the same time. Our treatment resulted in at least a doubling of total clutch size in the nest when found. We chose three eggs because data on natural parasitism for both species indicated >70% of all parasitized nests in our population contained three or fewer eggs (Dugger 1996). Control nests received no extra eggs, but were visited with the same frequency as treatment nests to equalize researcher disturbance. Eggs from all nests were individually marked for later identification. All nests were monitored during laying (every 1–2 days) and incubation (once per week) to determine final host clutch-size and to record the fate of each egg at hatch. Searches were conducted in the surrounding vegetation during nest visits to locate displaced eggs.

From 1972–1991, nests were located in a fashion similar to 1992–1993. However, transects were searched only two to three times each season during mid-May to mid-June. In addition to these systematic searches, additional nests were found during daily visits to the study plots to monitor existing nests. Information recorded for all nests in all years included date found, incubation stage determined by floatation (Westerkov 1950) or candling (Weller 1956), and status (parasitized or not parasitized). Nest initiation date was determined by back-dating from when the nest was found, correcting for the number of parasitic eggs present in the nest. Laying rate (one per day) was based on data on over 300 laying events (P. Blums and B. Dugger unpubl. data).

We used several techniques to detect eggs laid by parasites. Differences in egg shape, color, and size or differences in duckling appearance were sufficient to identify the parasitic eggs or young of other species (the two species commonly parasitize each other). We identified conspecific brood parasitism by (1) egg accretion rates greater than one per day; (2) differences in egg size, shape, and color; (3) staggered incubation stages among eggs in a clutch late in incubation of greater than 3–4 days; (4) total clutch size >14 for Tufted Ducks and >13 for pochard; and (5) nests with eggs found outside the nest bowl. Maximum nonparasitized clutch size was determined using life-history data of long-living individuals (869 female Tufted Ducks and 1,196 pochards) which were captured 2–13 breeding seasons over their lifetime. Maximum clutch size was defined as the largest clutch size with no signs of brood parasitism that occurred at least twice during the lifetime of a female. Criterion 5 was created after data on marked eggs in known parasitized nests indicated that finding eggs outside the nest bowl primarily occurred at parasitized nests. Even if some nests were misclassified us-

ing this technique, the number of nests where this was the sole means of detecting parasitism was small (<3%). Both criteria 4 and 5 were only useful for detecting parasitism, not for measuring its intensity (defined as the number of parasite eggs per host nest). These techniques were applied by the same small number of people each year. DNA fingerprinting analyses of 15 complete clutches (8 classified as parasitized, 7 as not parasitized) indicated the combination of these techniques were 87% accurate (one nest in each category misclassified; P[non|par] = 12.5%, P[par|non] = 14.3%; B. Dugger unpubl. data].

In all years, we captured females during incubation using a drop-door nest trap (Blums et al. 1983). Band numbers of females recaptured from previous years were recorded. Unmarked birds were aged (1 vs. ≥2), using wing characteristics for pochards and a combination of wing and eye color characteristics for Tufted Ducks (Blums et al. 1996). They were fitted with metal leg bands before release. Nests were visited at hatch and ducklings were banded using plasticine-lined leg bands, which ducklings retained into adult life (Blums et al. 1994). Plasticine bands have lower loss rates and higher reporting rates than metal web tags and do not cause greater mortality to ducklings (Blums et al. 1999). Because most ducklings were banded and because females are philopatric in waterfowl, we knew the age of a large portion of breeding females.

During 1985–1991, ~3,000 eggs from nests in the marsh were brought to the field station and hatched in an incubator. Those ducklings were then banded and returned to nests on the study plots with newly hatched ducklings (but not to the nests from which they came). Return of those ducklings to natural nests effectively created parasitized nests. Because the band numbers of incubator-hatched ducklings were recorded separately from band numbers of ducklings hatched naturally in the nest, we were able to compare recruitment of host ducklings in parasitized nests to recruitment of ducklings from nonparasitized nests.

Data analysis.—Using nests from egg addition experiments in 1992–1993, we compared final clutch size, nest fate, and hatch success between parasitized females (treatment) and nonparasitized females (control). For treatment nests, only eggs laid by hosts were included in analyses. Hatching success, calculated only for successful nests, was defined as the percentage of host eggs that hatched. For analysis of nest success, nests were classified as either successful (at least one egg hatched) or failed. Failed nests included those abandoned and depredated.

We used likelihood ratio chi-square tests to compare egg loss and female age composition between control and treatment groups. We conducted ANOVA on ranked data to compare clutch size and hatch success between treatment and control groups. Interpretation of all ANOVAs was based on Type III

sum of squares (SAS Institute 1989). We used logistic regression (PROC CATMOD, SAS Institute 1989) to compare nest fate (success vs. fail) between treatment and control nests. Explanatory variables for ANOVAs and logistic regressions included year, species, and group (nonparasitized vs. parasitized). Initiation date and female age were not included after preliminary analyses confirmed there were no differences in mean initiation date or female age distributions between control and treatment nests for either species.

Recruitment was also a binomial response variable. Each nest attempt was classified as either successful (defined as returning one or more female ducklings from a nest in year i to the study area in year ≥[i + 1]) or unsuccessful. The treatment group included those nests showing no signs of natural parasitism that had ducklings added on the day of hatch. The control group contained nests that showed no signs of natural parasitism (based on criteria above). We used logistic regression (PROC CATMOD, SAS Institute 1989) to compare recruitment between conspecifically parasitized nests (host ducklings only) and nonparasitized nests. Additional explanatory variables included in models to control for potentially confounding factors were standardized hatch date, brood size (defined as the number of host species ducklings that left the nest), and female age (1 vs. ≥2). We did not attempt to calculate an unbiased estimate of recruitment rate, rather we focused on testing potential differences between parasitized and nonparasitized nests. Thus, we needed to assume only that detection probability was similar for recruiting birds of parasitized and nonparasitized nests.

Using the larger data set collected during 1972–1991, we compared nest success (successful or failed), adult female survival, and relative change in nest initiation date (year i to year i + 1) between parasitized and nonparasitized females. To control for interyear variation in initiation dates, nest initiation date and hatch date were standardized across years by subtracting individual nest dates from the yearly median date for each species.

We used logistic regression to compare nest success (defined as above) between parasitized and nonparasitized nests. We assumed different types of parasitism (intra- vs. interspecific) had similar effects on nest success, thus all types of parasitism (intra-, inter-, both intra- and interspecific) were included in the parasitized category. Because many nests were found already depredated or abandoned and it was impossible to reliably determine the status of those nests (parasitized or not parasitized), we only used nests that were active when found. Although that biases our point estimates, we were interested only in comparing relative difference in that parameter between nest status groups, not in calculating an unbiased estimate of nest success. The larger sample

size in this data set provided an opportunity to test for intensity-specific effects of parasitism on nest success (i.e. effect dependent on the number of parasitic eggs in the nest). Nests were placed into one of four categories (1) no parasitic eggs, (2) 1–3 parasitic eggs, (3) 4–6 parasitic eggs, and (4) >6 parasitic eggs. Additional explanatory variables in the analyses included standardized initiation date and nest-owner clutch size. Female age was not included in nest success analyses because only females captured just before hatch (thus, after most nest failures were likely to occur) could be aged. Because we were interested in separately comparing depredation and abandonment between groups, we conducted two analyses. In the first, nests were either successful or destroyed (abandoned nests not included); in the second, successful versus abandoned.

Females of both study species that nest relatively late in the breeding season experience lower reproductive success (P. Blums unpubl. data). As an indirect test to estimate if brood parasitism may influence future reproductive success, we compared standardized nest initiation dates between consecutive years ($i, i + 1$). Specifically, we compared mean change in nest initiation date (year i—year $i + 1$) of known individuals whose nests were classified as parasitized or nonparasitized in year i (1972–1991). Only first nests were used in these analyses. We used ANOVA and included nest fate in year i (successful vs. unsuccessful), female age (1, ≥2), nest status (parasitized vs. not parasitized), and standardized nest initiation date in year i as explanatory variables.

We used multistate capture–recapture models to compare annual adult female survival (Brownie et al. 1993, Nichols and Kendall 1995). Such models differ from standard capture–recapture models (e.g. Pollock et al. 1990) by allowing an individual to change status (e.g. parasitized in year i, but not parasitized in year $i + 1$) between sampling periods (years). Specifically, we used MSSURVIV (Brownie et al. 1993, Hines 1994) to test for differences in survival between parasitized and nonparasitized adult females (1975–1991). Because multistate models require large data sets, we assumed type of parasitism would not affect survival and included all parasitized nests (intra- and interspecific) in analyses.

Earlier survival analyses indicated yearling pochards had lower survival than birds ≥2, whereas no age-related differences in survival were detected for Tufted Ducks (Blums et al. 1996). To control for that source of variation, we excluded information collected on all yearling pochards (capture-histories begin with age 2). To control for potential covariation of survival, nest initiation date, and probability of being parasitized (Dugger 1996), our state variable incorporated nest status and nest initiation date. Thus, we compared survival among four states: early parasitized (parasitized nests initiated prior to the yearly median), early nonparasitized, late parasitized

(parasitized nests initiated ≥the yearly population median), and late nonparasitized.

Model selection involved two steps. First, goodness-of-fit G statistics, likelihood-ratio tests, and Akaike's Information Criteria (AIC) values were used to select the best model among three general models provided by MSSURVIV (Model A = time- and state-specific survival, transition, and capture probabilities; Model B = time-constant, state-specific survival and transition probabilities, but time- and state-specific capture probabilities; and Model D = time-constant, state-specific survival, transition, and capture probabilities). These models represented different hypotheses about temporal variation in model parameters but all were general with respect to state effects, that is all included state-specificity of all model parameters.

Having chosen the most appropriate general model (A, B, or D) for each species, we then formally tested the hypothesis that brood parasitism had no effect on adult survival by computing likelihood-ratio tests between the general model and a more restrictive (nested) model. The restrictive model allowed survival and transition probabilities to vary between early and late season, but survival and transition probabilities between parasitized and nonparasitized females were held constant within seasonal categories. A significant between-model test result indicated the additional parameters included in the more general model (H_a) better described the data (i.e. survival and transition probabilities were different between parasitized and nonparasitized birds).

RESULTS

During 1992–1993, 75 Tufted Duck and 63 pochard nests were found with <4 eggs. The age distribution of females captured during incubation did not differ between control and treatment group for either pochards ($\chi^2 = 0.49$, df = 1, $P = 0.48$) or Tufted Ducks ($\chi^2 = 0.35$, df = 1, $P = 0.60$). Mean clutch size differed between species ($F = 5.87$, df = 1 and 92, $P = 0.02$), but not between parasitized and nonparasitized nests ($F = 150$, df = 1 and 92, $P = 0.10$; Table 1). No host eggs went missing from nonparasitized pochard nests ($n = 15$ nests), whereas two host eggs disappeared from each of two parasitized pochard nests (10%, $n = 20$ nests). For Tufted Ducks, one egg disappeared from two parasitized ($n = 28$) and two nonparasitized ($n = 31$) nests. No significant interaction terms resulted from hatch success ANOVAs ($P > 0.30$). Using only a main effects model, hatch success was similar between species ($F = 1.27$, df = 1 and 90, $P = 0.26$), years

TABLE 1.   Comparisons of host reproductive parameters between experimentally parasitized (three eggs added before hosts laid fourth egg) and nonparasitized nests of Common Pochards and Tufted Ducks breeding on Engure Marsh, Latvia, 1992–1993.

Species	Nest status	Parameter		
		Clutch size $x \pm$ SE (n)	Nest success % (n)	Hatch success (%) $x \pm$ SE (n)
Common Pochard				
	Parasitized	7.6 ± 0.3 (20)	64.5 (31)	93.0 ± 1.1 (20)
	Nonparasitized	7.9 ± 0.2 (19)	65.4 (26)	92.0 ± 2.9 (15)
Tufted Duck				
	Parasitized	9.0 ± 0.2 (30)	76.9 (39)	94.9 ± 0.8 (28)
	Nonparasitized	9.2 ± 0.2 (33)	91.7 (36)	95.6 ± 0.7 (31)

($F = 0.10$, df $= 1$ and 90, $P = 0.75$), and parasitism state ($F = 0.49$, df $= 1$ and 90, $P = 0.48$; Table 1).

Of nests used in the egg addition experiment, no Tufted Duck nests and only five (8%) pochard nests were depredated during both years of study. These were too few for cause-specific analysis; therefore, comparisons of nest success probabilities were based only on successful and abandoned nests. Nest abandonment was common for both species (Table 1) and in almost all cases, abandonment occurred after the first nest visit. Nest success differed between species ($\chi^2 = 7.74$, df $= 1$, $P = 0.02$). Tufted Ducks had higher overall nest success than pochards (Table 1). However, nest success did not vary between parasitized and nonparasitized nests ($\chi^2 = 1.23$, df $= 1$, $P = 0.27$).

For the larger observational data set collected from 1972–1991, nonparasitized pochard nests were depredated slightly more often than parasitized nests ($\chi^2 = 21.9$, df $= 3$, $P = 0.0001$; Table 2). Percent of depredated nests did not differ between nonparasitized and parasitized nests for Tufted Ducks ($\chi^2 = 6.05$, df $= 3$, $P = 0.11$), but trends were similar to pochards. Probability of nest abandonment differed with parasitism intensity for pochards ($\chi^2 = 9.36$, df

$= 3$, $P = 0.025$); however, differences were not between nonparasitized nests and nests with >6 eggs ($P > 0.10$), but rather between nests with >6 eggs and the other two parasitism categories. Nests with >6 parasitic eggs were abandoned more often for Tufted Ducks ($\chi^2 = 14.8$, df $= 3$, $P = 0.002$; Table 2).

For our subsample of all possible nests, the probability of recruiting at least one female duckling from a successful nest into the breeding population was 13.3% for pochards ($n = 836$ nests) and 9.6% for Tufted Ducks ($n = 450$ nests). Including female age, hatch date, and brood size in models for both species, parasitism had no detectable effect for either pochards (12.8% [parasitized] vs. 13.5% [nonparasitized], $P = 0.06$) or Tufted Ducks (9.3% [parasitized] vs. 9.6% [nonparasitized], $P = 0.44$).

We used 1,196 pochard and 872 Tufted Duck female capture histories to model survival. Initial comparisons indicated model B (time-constant, state-specific survival and transition probabilities but time-dependent capture probabilities) was the most appropriate model for pochards; whereas, model D (time-constant, state-specific survival, transition, and capture probabilities) was most appropriate for Tufted Ducks. These models served as the alternative

TABLE 2.   Influence of differing levels of brood parasitism on host nest success (%) for Common Pochards and Tufted Ducks nesting at Engure Marsh, Latvia, 1972– 1993.

Species	Nest fate	Nonparasitized	Number of parasitic eggs		
			1–3	4–6	>6
Common Pochard	Successful	91.7	95.7	95.9	91.2
($n = 4,776$)	Abandoned	2.9	2.1	2.6	5.7
	Depredated	5.4	2.2	1.5	3.1
Tufted Duck	Successful	92.8	95.4	95.9	88.4
($n = 2,854$)	Abandoned	3.2	3.1	2.1	10.5
	Depredated	4.0	1.5	2.0	1.1

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TABLE 3. Likelihood-ratio tests of the null hypothesis (H_o) that annual survival ϕ of adult females is not affected by brood parasitism (H_a). Data are for female Common Pochards and Tufted Ducks breeding at Engure Marsh, Latvia, 1975–1993.

(H_o vs. H_a)[a]	Statistic χ^2 (df, P)	Survival values				Transition[d]	
		H_o		H_a			
		State[b]	ϕ (SE)	State[c]	ϕ (SE)		
Common Pochard							
B_r vs. B	1.7 (2, 0.43)	E	0.646 (0.016)	E^{np}	0.667 (0.038)	E^p	0.380 (0.524)
						L^{np}	0.178 (0.089)
						L^p	0.152 (0.064)
				E^p	0.620 (0.041)	E^{np}	0.291 (0.575)
						L^{np}	0.162 (0.078)
						L^p	0.147 (0.063)
		L	0.618 (0.018)	L^{np}	0.617 (0.034)	E^p	0.263 (0.361)
						E^{np}	0.224 (0.441)
						L^p	0.192 (0.084)
				L^p	0.620 (0.031)	L^{np}	0.275 (0.127)
						E^{np}	0.193 (0.385)
						E^p	0.258 (0.350)
Tufted Duck							
D_r vs. D	5.7 (2, 0.06)	E	0.746 (0.016)	E^{np}	0.720 (0.024)	E^p	0.269 (0.596)
						L^{np}	0.277 (0.138)
						L^p	0.045 (0.145)
				E^p	0.761 (0.027)	E^{np}	0.348 (0.064)
						L^{np}	0.226 (0.117)
						L^p	0.044 (0.140)
		L	0.634 (0.016)	L^{np}	0.599 (0.029)	E^p	0.174 (0.035)
						E^{np}	0.264 (0.048)
						L^p	0.067 (0.216)
				L^p	0.700 (0.039)	L^{np}	0.494 (0.223)
						E^{np}	0.234 (0.060)
						E^p	0.202 (0.057)

[a] Model designations: B = time(year)-constant, state-specific survival and transition probabilities but time-specific capture probabilities; B_r = survival rates allowed to vary between early and late seasonal category, but within season category, survival of parasitized and nonparasitized females held constant. D = time-constant, state-specific survival, transition, and capture probabilites; D_r = analogous to B_r.

[b] E = nests initiated prior to yearly population median, L = nests initiated on or after yearly population median.

[c] Superscript designations: np = nonparasitized, p = parasitized.

[d] Transition probabilities (SE); probability of moving from the state specified under H_a in year i to different state in year $i + 1$. The probability of remaining in the same state calculated as $1-\Sigma$ (other three values). Parameter estimates reported from reduced model (survival constant between parasitized and nonparasitized females).

hypothesis (H_a) for hypothesis testing with restrictive models. Between-model likelihood-ratio tests indicated parasitism had no affect on survival or transition probabilities of pochard females (Table 3). However for Tufted Ducks, between-model tests indicated that survival of parasitized females was higher than survival for nonparasitized females (Table 3).

When controlling female age, nest fate, and nest initiation date in year i, we detected no difference in mean relative changes in nest initiation dates between parasitized and nonparasitized female pochards ($F = 0.08$, df = 1 and 991, $P = 0.78$). However, for Tufted Ducks, mean relative change in nest initiation date did differ between parasitized (-0.5 ± 0.6 days) and nonparasitized females (-4.3 ± 0.3 days;

$F = 7.3$, df = 1 and 708, $P = 0.007$). Parasitized Tufted Ducks nested relatively later in year $i +$ 1 (3.8 days) than nonparasitized females.

DISCUSSION

Prehatch costs of brood parasitism to host females may include reduced clutch size, nest success, and hatching success of host eggs. Based on egg-addition experiments, neither pochards nor Tufted Ducks suffered prehatch costs associated with conspecific brood parasitism. We detected no difference in clutch size, hatch success, or nest success between parasitized and nonparasitized females. Amat (1985) reported lower hatch success in Common Pochard nests parasitized by Red-crested Po-

chards (*Netta rufina*). He attributed increased mortality to inefficient incubation of enlarged clutches, which resulted in more dead embryos. Common Pochard clutch sizes were similar between our studies as was the mean number of parasitic eggs per nest (3.0 vs. 2.5); however, some naturally parasitized pochard nests in Amat's study had as many as nine parasitic Red-crested Pochard eggs. Higher embryo mortality at parasitism intensities above the three-egg level used in our experiment might account for the difference between studies. No such relationship was found for Canvasback (*Aythya valisineria*; Sorenson 1997). Alternately, Amat did not account for conspecific nest parasitism in his analysis, which may have resulted in significantly more nonterm Common Pochard eggs at hatch. Amat also did not test for a correlation between seasonal trends in embryo mortality and parasitism rate.

Host-egg displacement into the water during parasitic events was a significant cost resulting from intraspecific parasitism of Canvasback nests (Sorenson 1997). Because we added eggs to nests, we minimized host–parasite interaction at the nest and were therefore unable to evaluate this aspect. However, in contrast to Canvasbacks (which nest over water) our experiments were conducted on islands, increasing the likelihood females could recover displaced eggs.

Although not statistically significant, the 15% lower nest-success estimate for parasitized Tufted Duck nests seems large enough to be an important selective force shaping host behavior towards parasites. Unfortunately, the influence of such desertions on host fitness is difficult to estimate. If abandoning females do not renest, costs would be high. Females were not captured and identified prior to abandonment, so we could not directly estimate renesting rates. However, because most abandonment occurred during laying, females had a high probability of renesting (P. Blums unpubl. data). Assuming females renested, fitness reductions would be limited to differences between first and second efforts.

Using the larger data set, we detected greater abandonment only for Tufted Duck, but only when nests contained >6 parasitic eggs. This supports the hypothesis that parasitism's affect is conditional on its intensity (Weller 1959, Sorenson 1997). Previous analysis indicated fe-

males who abandoned nests late in incubation weighed less than females who successfully hatched clutches for both species (~25 g for birds ≥2 years old; Blums et al. 1997). Thus, there may be a cost associated with incubating large numbers of parasitic eggs (Gloutney and Clark 1991, Hepp et al. 1990). However, our test benefited from large sample sizes. The actual difference between our estimates was small and possibly of limited biological importance. Furthermore, the probability of a nest being parasitized at such a high level (calculated as probability of being parasitized × probability of >6 eggs in parasitic nest), was low for pochards (4.5%) and Tufted Ducks (3.2%). Thus, at best a small percentage of females (<1% both species) potentially suffered costs associated with incubating parasitic eggs.

Potential posthatch costs of brood parasitism include lower duckling recruitment, lower over-winter adult survival, and subsequent-year reductions in reproductive success. Duckling recruitment was not different between parasitized and nonparasitized nests for either pochards or Tufted Ducks. Additionally, parasitism had no detectable effect on pochard adult survival or between-year nest initiation dates. Our results are consistent with studies on ducks and geese that report no difference between parasitized and nonparasitized nests in adult survival (Lessells 1986, Eadie 1989, Lank et al. 1990, Rohwer and Heusmann 1991; although those studies did not use a multistate modeling approach), survival of young to fledging (Clawson et al. 1979, Eadie 1989, Milonoff and Paananen 1993, Sorenson 1997), recruitment of young into the breeding population (Lank et al. 1990) or year $i + 1$ fitness components (Lessels 1986, Williams et al. 1994). Only Andersson and Eriksson (1982) reported Common Goldeneye (*Bucephala clangula*) duckling survival was lower in larger broods. This is contrary to other work on waterfowl (Rohwer 1992). Milonoff et al. (1995) recently demonstrated that Andersson and Eriksson's finding was probably biased by methodological problems.

Some of our results for Tufted Ducks were contrary to those for pochards and for other studied species. First, parasitism of female Tufted Ducks in year i was associated with a slight delay in nest initiation dates in year $i +$ 1 relative to nonparasitized females. Without

direct estimates of year $i + 1$ fitness compo-
nents, we suggest it is difficult to characterize
a 3.8 day delay in nest initiation as a biologi-
cally important cost to females. Second, we de-
tected differences in adult Tufted Duck surviv-
al between parasitized and nonparasitized
females. However, instead of suggesting costs
to hosts, survival estimates of parasitized fe-
males were higher than nonparasitized fe-
males. It is unlikely that parasitism could in-
crease the survival of host females. A more
likely explanation is parasites more frequently
parasitized high-quality hosts that generally
survived better. Such an explanation is con-
sistent with data indicating older females are
parasitized more frequently than yearlings for
pochards and Tufted Ducks, even after con-
trolling for potentially confounding variables
(Dugger 1996). However, earlier survival com-
parisons failed to detect age-related differences
in survival for Tufted Ducks (Blums et al.
1996). Thus, if differences in host quality exist,
they are not simply correlated with female age
for Tufted Ducks.

Moderate levels of brood parasitism had lit-
tle effect on the reproductive success of Com-
mon Pochards and Tufted Ducks, suggesting
the more neutral "prehatch brood amalgam-
ation" may be a more appropriate term to de-
scribe this behavior in those species (Eadie et
al. 1988). Consistent with our conclusion (but
not necessarily a direct corollary, see Sorenson
1997), females for both species made no obvi-
ous attempts to discriminate against parasitic
eggs once they had been added to the nest
(Dugger et al. 1999). Data for other species with
precocial young including Ostrich (*Struthio ca-
melus*; Bertram 1979), fish (McKaye 1985), and
insects (J. Eadie unpubl. data) indicate the re-
sults for our study are generally consistent
with those from other taxa with precocial
young. Work investigating the frequency and
effect of host–parasite interactions at the nest
would be helpful to complete the picture for
Tufted Duck and Common Pochard.

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Associate Editor: L. M. Smith