Host response to brood parasitism in two species of diving duck

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We used egg addition experiments and naturally parasitised nests of Common Pochard Aythya ferina and Tufted Duck A. fuligula to look for three host responses to brood parasitism; nest abandonment, egg discrimination, and between-year nest site movement. Parasitised females did not abandon nests more often (P = 0.26), discriminate against parasite eggs (P's ≥ 0.38), or move their nests a greater distance (P's ≥ 0.39) than non-parasitised females for either species. Host female Common Pochards and Tufted Ducks do not discriminate against parasitic eggs once they are added to the nest.

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Brood parasitism reduces host reproductive success in many bird species (Payne 1977). Such costs create selective pressures on hosts to minimise the impact of parasitism (Rothstein 1990). Host responses to parasitism include egg ejection (Rothstein 1975), nest guarding (Burgham & Picman 1989), clutch reduction (Power *et al.* 1989), secretive behaviour around nests (Uyehara & Narins 1995), burying parasitic eggs (Hobson & Sealy 1987), and nest abandonment (Fenske & Burley 1995). Most documented examples involve interspecific parasitism of altricial species that provide extensive post-hatch parental care to offspring (Rohwer & Freeman 1989; Rothstein 1990).

Less is known about anti-parasitism behaviour in precocial species such as waterfowl, but reported host responses include nest site defence (Mineau & Cooke 1979; Gauthier 1987), displaced eggs (Mallory & Weatherhead 1993) and nest abandonment (Andersson & Eriksson 1982; Eadie 1989). The types of responses may vary among individuals (eg Canvasbacks [*Aythya valisineria*]; Nudds 1980; Sayler 1996; Sorenson 1997) or be dependent on the level (Andersson & Eriksson 1982; Eadie 1989) or timing of parasitism (Sorenson 1997).

The relative lack of data for waterfowl may relate to difficulties involved with directly observing host/parasite interactions or difficulties distinguishing

between parasite and host eggs. However, lack of data may also reflect tacit support for the hypothesis which states brood parasitism has little impact on host fitness in precocial species (Rohwer & Freeman 1989). If true, precocial hosts are under little selective pressure to develop anti-parasite behaviours. Given host reactions to parasitic eggs have implications for the evolution of brood parasitism (Eadie et al. 1988), more data on host responses in waterfowl are needed. Here, we use egg addition experiments and naturally parasitised nests of Common Pochard (Aythya ferina; hereafter pochards) and Tufted Duck A. fuligula to look for three possible host responses to parasitism; nest abandonment, egg discrimination, and between-year nest site movement.

Study Area and Methods

Research was conducted on Engure Marsh, Latvia, Eastern Europe. Engure Marsh is a 35-km² shallow, permanently-flooded, palustrine wetland located on the east coast of the Baltic Sea (57°15'N, 23°07'E). Females placed their nests on land and vegetation islands located throughout the marsh. See Blums et al. (1997) for a more detailed description of the study area.

We added eggs to nests to test for differences in nest abandonment rates between parasitised and non-parasitised females and to look for egg discrimination behaviour by hosts. We located nests by systematically walking habitats in parallel transects every 4-6 days during May and June 1992-93. Nests found with less than four eggs that showed no signs of natural parasitism (see below) were alternately assigned to either the treatment or control group. Treatment nests received three conspecific eggs added all at once before the fourth host egg was laid. No eggs were added to control nests. All eggs were individually marked for later identification. Both control and treatment nests were revisited at least every other day during laying and several times during incubation to check for displaced or missing eggs and to determine nest fate. All nests were visited on each trip to study plots, therefore visitation frequency was similar between control and treatment group. We used logistic regression to test for differences in nest abandonment including both species and year as independent variables.

In 1993, during the first week of incubation, we moved treatment eggs to the centre of each nest to test if hosts displaced parasite eggs to the clutch periphery. Nests were revisited four days later to record the position of each egg as central (surrounded on all sides by eggs) or peripheral (at least one side of egg against nest edge). To assure that initial egg placement did not influence results, after recording the position of each egg during the first revisit, all parasitic eggs were then moved to the clutch periphery and nests were checked four days later (Mallory & Weatherhead 1993). To test host response to interspecific parasitism, three Mallard Anas platyrhynchos eggs were added to 10 pochard nests in 1993. Procedures were identical with the above experiment except that Mallard eggs were added during the first week of incubation.

We used a Sign test to compare the observed number of parasite eggs located centrally to the expected number assuming random egg placement. If hosts discriminated against parasite eggs, we predicted more parasite eggs than expected would be located on the nest periphery. We calculated expected values

by multiplying the proportion of the total clutch (host + parasite eggs) occupying centre positions to the number of parasite eggs in the nest. For example, if four parasite eggs were added to a host clutch of eight and three eggs were located in the centre of the clutch, the expected number of parasite eggs located centrally equals $(3/12) \times 4$ or 1.0.

We used data gathered during 1959-95 to compare between-year nest site movement between parasitised and non-parasitised females. Nest searching procedures during 1959-95 were similar to those in 1992-93, but searches were conducted only two to three times per season. Thus, most nests (ca. 79%) were found after incubation had begun. Parasitised nests were identified using: 1) differences in egg size, colour, and shape, 2) within-clutch variation of three or more days in incubation stage, 3) total clutch size ≥13 for pochards and >14 for Tufted Duck,

and/or 4) egg accretion rates > one per. DNA fingerprinting analyses of 15 complete pochard clutches (adult + eggs) suggested these techniques resulted in about a 13% misclassification of nests (one nest in each category was misclassified, B. Dugger unpubl. data). Females were captured during the last week of incubation to record the band numbers of recaptured females. The location of each nest was mapped (most to within 1 or 2 m) at the end of each nesting season. Linear distances between nests in consecutive years was used as a measure of nest site movement. We used analysis of variance to compare mean between-year nest movement. In addition to nest status (parasitised vs. not parasitised), year, nest fate (successful vs. failure), female age (1 vs. ≥ 2), and standardised nest initiation date (Blums et al. 1997) were included as covariates for analysis.

Table 1. Abandonment rates (%) and distance (m) moved (mean ± SE) between consecutive yearly nest attempts for parasitised and non-parasitised Common Pochards and Tufted Ducks nesting on Engure Marsh, Latvia. Sample sizes in parentheses.

	Common Pochard		Tufted Duck	
	Para	Not Para	Para	Not Para
Abandonment[a]	35.5	34.5	23.1	8.3
	(31)	(36)	(39)	(36)
Distance moved[b]	248±27	254±23	236±25	211±15
	(555)	(774)	(401)	(1,035)

[a] Data from egg addition experiments in 1992-93

[b] Data from 1959-95

Results

Nest abandonment differed between species (χ^2 = 5.07, P = 0.02; **Table 1**), but not between experimentally parasitised and non-parasitised nests (χ^2 = 1.23, P = 0.26) for either species (species by nest status interaction term; χ^2 = 1.47, P = 0.22). Egg position within the nest was independent of egg origin for both Tufted Ducks (host vs. conspecific parasite; P = 0.38, n = 6) and pochards (host vs. conspecific eggs; χ^2 = 1.95, P = 0.51, n = 9; host vs. interspecific eggs - χ^2 = 0.14, P = 1.0, n = 10). Combining all nests into one sample, half the nests had slightly more parasitic eggs than expected and half had fewer eggs than expected in centre positions. 16 per cent of pochard nests (n = 34) and 9.8% of Tufted Duck nests (n = 59) lost at least one egg. The proportion was higher in parasitised nests than control nests for both pochards (26% vs. 13%) and Tufted Ducks (15% vs. 6%), but not statistically different (P's > 0.40). For each species, three of four eggs that could be assigned belonged to hosts. No eggs were lost from pochard nests experimentally parasitized with Mallard eggs. Controlling for year, nest fate, female age, and nest initiation date, mean between-year nest movement was independent of nest status for both pochards (P = 0.87) and Tufted Ducks (P = 0.39; **Table 1**). Too few females involved with the egg addition experiments were recaptured to permit a comparable analysis.

Discussion

Nest abandonment by waterfowl may be an adaptive response by females to avoid the costs of caring for unrelated young (Andersson & Eriksson 1982; Rohwer & Freeman 1989). The higher abandonment rates of parasitised nests reported in many studies would seem to support this hypothesis (eg Weller 1959; Jones & Leopold 1967; Bezzel 1969; Clawson et al. 1979; Eadie 1989). However, inferring cause-and-effect has been difficult because most studies were not experimental (Dugger 1996). Furthermore no studies have attempted to distinguish between abandonment as a host response (ie abandon shortly after parasitism occurs) vs. abandonment as a cost of parasitism. In the latter case, females may incubate the parasitised clutch for several weeks prior to abandoning the nest.

All but two occasions of nest abandonment by pochards and Tufted Ducks in the treatment group occurred immediately after experimental eggs were added to the nest, consistent with anti-parasite behaviour. However, desertion rates were similar for control and treatment nests; thus, abandonment seemed more a general response to disturbance during laying rather than a specific response to parasitism. Our results were similar to experimental work on Goldeneye nests with < 17 total eggs (Eadie 1989) and < four parasite eggs (Andersson & Eriksson 1982). In those studies, abandonment rates increased when total clutch size exceeded 16 eggs or when seven parasite eggs were added to nests all at once. Large numbers of parasitic eggs do occur in naturally parasitised pochard and Tufted Duck nests (Hilden 1964; Bezzel 1969; Newton & Campbell 1975; Amat 1985; Dugger 1996), and this has been correlated with increased nest abandonment suggesting host response may be conditional on the level of parasitic egg addition, but additional experiments are necessary to

infer cause-and-effect. Clutch sizes >16 eggs and parasitism intensity ≥ seven eggs are common for species using artificial nest boxes (eg Clawson et al. 1979; Haramis & Thompson 1985), which may explain the higher abandonment rates reported in those studies.

Even if hosts do not abandon nests, females may eject parasitic eggs from the nest (Rothstein 1975; Bertram 1979). While losses in our study were somewhat more frequent in parasitised nests, the majority of eggs lost from nests belonged to hosts, suggesting egg loss was related to factors other than parastism. Amat (1985) reported that Common Pochards recognised and discarded parasitic eggs laid by Red-crested Pochards (Netta rufina). However, his results seem consistent with ours at the moderate parasitism levels used in our experiment (based on Amat's [1985] Figure 2). Beyond this observation, results are difficult to compare because Amat analysed nests found during incubation and did not individually mark eggs in the nest, which we found can lead to confusion about the origin of eggs found outside the nest (B. Dugger pers. obs.).

Rather than eject eggs, hosts may respond to parasitism by displacing suspected parasite eggs to the clutch periphery. Displacement is less risky than ejection because it lowers the cost of recognition errors (Sayler 1992). Eggs on the periphery are often relatively cooler (Drent 1975; Sayler 1992), possibly reducing hatching success. Our results, and those for Goldeneye (Eadie 1989), Canvasbacks (Sayler 1996; Sorenson 1997) and one study on Hooded Mergansers (Dugger et al. 1999) indicated parasitic eggs were not more likely to be on the nest periphery than host eggs. These results differed from another study on Hooded Mergansers (Lophodytes cucullatus), which reported females discriminated against the eggs of Common Goldeneye (Mallory & Weatherhead 1993). Egg discrimination in that study may have been facilitated by the color difference between Merganser and Goldeneye eggs (Mallory & Weatherhead 1993) but additional work is needed to test alternate explanations (Dugger 1999).

Finally, rather than discriminate against parasite eggs after they have been laid in the nest, host females may attempt to avoid repeated parasitism by moving nest sites between years. Nest site change has been documented in response to failed breeding attempts in waterfowl (Eadie 1989; Hepp & Kennamer 1992), but not as a response to parasitism. Even with our large sample, we found the average distance moved between yearly nest attempts did not differ between parasitised and non-parasitised females.

We were unable to observe host behaviour prior to and during a parasite's attempt to lay an egg, but our results indicated female Tufted Ducks and Common Pochards did not respond to parasite eggs once they were added to the nest. Furthermore, females did not attempt to avoid repeated parasitism by moving next year's nest further than unparasitised females. Power calculations using our sample sizes, the parameter values for non-parasitised nests, alpha = 0.05, and beta = 0.20 suggested we could reliably detect relative differences of 55% in nest abandonment, 100 m in movement, and 50% for egg position analyses. In all cases, measured differences were less than the detectable effect size, thus, it is important to consider whether important biological differences went undetected. We believe no such meaningful differences were evident for the movement (**Table 1**)

or egg position analysis (ie plotted data indicated 50% of nests fell above and below expected value). The difference in abandonment rates for parasitised Tufted Ducks suggests some females may respond to brood parasitism by abandoning nests. At best, such a reaction was inconsistent since 75% of parasitised hosts remained with parasitised nests. Additional research with larger samples or new research contrasting birds that abandon to those that do not may help resolve whether the difference in abandonment by parasitised females is real or an artifact of sampling. Experiments using a larger number of added eggs are needed to test if host behaviour is conditional on the level of parasitism as has been reported elsewhere (Andersson & Eriksson 1982).

Acknowledgments

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