



Original Article

Environmentally driven escalation of host egg rejection decimates success of an avian brood parasite

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The black-headed duck (*Heteronetta atricapilla*) of South America is the only known avian obligate brood parasite with precocial offspring. In Argentina, it relies on two species of coots as primary hosts, which typically reject 35–65% of duck eggs. We show that environmentally driven increases in host egg rejection behavior lead to substantial reductions in the reproductive success of the brood parasite. Episodes of flooding and vegetation loss caused dramatic shifts in host egg-rejection behavior, resulting in rejection (85–95%) of almost all duck eggs. Coots respond to fluctuating water levels by building up their nest, raising their own eggs but leaving duck eggs behind. Coots can apparently recognize parasitic duck eggs, but large-scale rejection is triggered only when hosts must actively make a choice. We use a simple population model to illustrate the unique demographic challenges that black-headed ducks face with their parasitic lifestyle and to explore the potential impact of environmentally induced escalation of egg rejection. Using the best available estimates for key vital rates, we show that obligate parasitism may provide a demographically precarious existence for black-headed ducks, even under benign environmental conditions. Environmentally mediated increases in egg rejection rates by hosts could impact significantly the viability of this enigmatic species of brood parasitic duck. Our results demonstrate that egg rejection rates are not fixed properties of host populations or individuals but are strongly influenced by social and ecological factors. Shifts in these environmental drivers could have important and unforeseen demographic consequences for brood parasites.

Key words: avian brood parasitism, black-headed duck, conservation behavior, egg rejection, environmental perturbation, host behavior, host–parasite coevolution, population dynamics, South American coots.

INTRODUCTION

The antagonistic interaction between brood parasites and their hosts often fuels coevolutionary arms races (Brooke and Davies 1988; Rothstein 1990; Thompson 1994). Avian brood parasites lay their eggs in the nests of other birds, which then provide all subsequent care to the parasite's offspring. The fitness costs to hosts can be considerable, resulting in natural selection for a diversity of host defensive traits to reduce the occurrence or costs of parasitism (Sealy 1995; Davies 2000; Spottiswoode and Stevens 2010; Yang et al. 2010). While there are a variety of tactics hosts adopt to make parasitism less likely, recognition and rejection of parasitic eggs after parasitism has occurred is the most widespread and well-studied host defense (Langmore et al. 2003; Grim 2007; Welbergen

and Davies 2009; Sato et al. 2010; Feeney et al. 2012; Gloag et al. 2013). The evolution of host defenses sets the stage for antagonistic coevolution—evolutionary counter-responses by the parasite to thwart host egg recognition and rejection (Brooke and Davies 1988; Rothstein 1990; Feeney et al. 2014).

Brood parasitism can also have demographic consequences for both hosts and parasites (May and Robinson 1985; Arcese et al. 1996; Woodworth 1999; Smith et al. 2002; Winfree et al. 2006; Jewell and Arcese 2008; Tryjanowski and Morelli 2015), but this topic has received far less attention. In extreme cases, the negative impacts of parasitism on host reproductive success can potentially devastate local host populations. Environmental change, such as habitat fragmentation, can further alter a species exposure to brood parasitism and result in declines in reproductive success below the threshold required for local population sustainability (Robinson et al. 1995).

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Conversely, brood parasitism can also have important implications for the dynamics of the brood parasite populations, but this is even less well studied than for host populations. Host specialists may be most vulnerable to environmentally induced changes in host behavior that negatively impact parasite reproductive success (Ducatez 2014). Indeed, some populations of specialist parasitic taxa have exhibited recent dramatic declines (Douglas et al. 2010; Thorogood and Davies 2013), prompting interest in the factors that regulate these parasite populations. One possibility is that environmental drivers, such as climate change, disrupt the degree of overlap between the breeding seasons of the parasite and their hosts (Saino et al. 2009; Møller et al. 2011), with possible negative consequences for the brood parasites due to reduced availability of hosts. Alternatively, changes in host behaviors, such as egg rejection, which negatively impact the success of brood parasites, could have cascading effects for population stability. It is now clear that egg rejection rates are not fixed properties of populations or even individuals but are influenced by both social and ecological factors (Davies et al. 1996; Thorogood and Davies 2013; Grim et al. 2014; Molina-Morales et al. 2014). However, the implications of the plasticity of host responses for parasite fitness and population dynamics remain unclear.

We examined the consequences of environmentally driven changes in host egg rejection behavior for the reproductive success of a specialized brood parasite, the black-headed duck (*Heteronetta atricapilla*). This South American species is the only avian obligate brood parasite with self-feeding young (Lack 1968; Weller 1968; Davies 2000). It is quite specialized in terms of important hosts—while its eggs have been documented in a variety of host species, 80% of the eggs in an Argentine population occurred in two species of coots (red-gartered *Fulica armillata* and red-fronted coots *Fulica rufifrons*), and almost 60% of the ducklings in the population hatched from nests of a single species, the red-gartered coot (Lyon and Eadie 2004, 2013). A geographic study of several Chilean populations of black-headed ducks showed that the densities of the brood parasite correlate with densities of these two species of coots, suggesting that they may be important throughout the range (Cofre et al. 2007).

Black-headed ducks may be particularly vulnerable to changes in the behavior of their two main hosts for two reasons: the hosts reject a substantial fraction of the duck eggs and the ducks appear unable to counter this egg rejection with an evolutionary response (Lyon and Eadie 2004). Several lines of evidence suggest that the hosts evolved egg rejection behavior to counter conspecific brood parasitism within their own species rather than interspecific parasitism from the ducks (Lyon and Eadie 2004). The ducks are thus trapped in the arms race of their hosts and their reproductive success is largely influenced by factors that affect egg rejection behavior by their hosts.

In addition, black-headed ducks are unique among the 100 species of obligate parasites in having precocial offspring, a life-history oddity with implications for both the evolution and persistence of an obligate parasitic lifestyle. Family size in precocial birds is thought to be limited by the ability to produce eggs since the offspring feed themselves, and so the potential for increased fecundity via emancipation of parental care is less clear for a parasitic duck (Lyon and Eadie 1991). Weller (1968) speculated that a wide diversity of hosts combined with high success with those hosts could explain the evolutionary advantage of parasitism for the black-headed duck. However, this idea was not supported by the discovery that the ducks depend on very few host species and that these hosts

reject a fairly high proportion of duck eggs (Lyon and Eadie 2004, 2013). Thus, the combination of a modest fecundity of a precocial bird and moderate egg rejection by hosts may make black-headed ducks more vulnerable to environmentally driven shifts in host-parasite interactions than some other brood parasites.

Here, we show that two environmental changes—flooding and loss of the emergent vegetation hosts use for nesting—dramatically alter host responses to the brood parasite eggs in their nests, with devastating consequences for the parasite's reproductive success. We examine changes in host rejection behavior during 3 years of field study. We then use a simple demographic model to explore the potential population consequences of these induced changes in host behaviors and find that under some scenarios, the viability of the brood parasite population is uncertain. Our study not only highlights the need for a much better understanding of the basic life history of the black-headed duck but further illustrates that host recognition behavior and parasite population dynamics could be fundamentally altered by rapidly changing environmental conditions.

METHODS

Study wetlands and species

We conducted detailed studies of the interaction between black-headed ducks and their two main hosts, red-gartered and red-fronted coots, on six different wetlands within 25 km of the town of General Lavalle, Buenos Aires province, Argentina, in three different years. Map locations of study wetlands, named in terms of the estancias (ranches) on which they are located, are provided in Lyon and Eadie (2013). The distance and compass bearings from General Lavalle, as determined with Google Earth (with the year of study in parentheses), are: Palenque 10 km at 196° (1994); Real Viejo Marsh A 18.9 km at 185° (1993, 1997); Real Viejo Marsh B 20.9 km at 180° (1993, 1997); Mal Abrigo Gull Marsh 19.2 km at 151° (1993); Mal Abrigo Tern Marsh 19.2 km at 148° (1993); and Cari Lauquen 21.7 km at 214° (1994).

We conducted systematic surveys of the marshes every 2–4 days on foot or by canoe to find potential host nests and detect brood parasitism. The vegetation was sufficiently sparse and the large nests conspicuous enough that we are confident that we found almost all nests of potential host species breeding on the study area. Nests were identified to species by observing birds on or near nests. Parasitism was easily detected because the duck eggs differ dramatically from the eggs of both major hosts (photos of host and duck eggs are available in Lyon and Eadie 2004, Figure 1D, and Lyon and Eadie 2013, Figure 1). On each visit, all new duck eggs were labeled with a Sharpie permanent-ink felt pen and previous eggs censused to determine their fate: rejected, depredated, hatched, or left unhatched after host chicks hatched. Coots rejected duck eggs (real and experimental) mainly by burying them in nesting material, but some were ejected from nests or simply disappeared. On a subset of wetlands, we assessed the density of emergent vegetation cover at each host nest by estimating the percentage of vegetation cover in each of the four 90° wedges (10 m radius) around each nest and calculated the average.

Egg rejection studies

Environmental effects on egg rejection were determined using four methods: natural cases of brood parasitism by the ducks (Mal Abrigo Gull and Tern Marshes and Real Viejo Marsh A, all 1993),

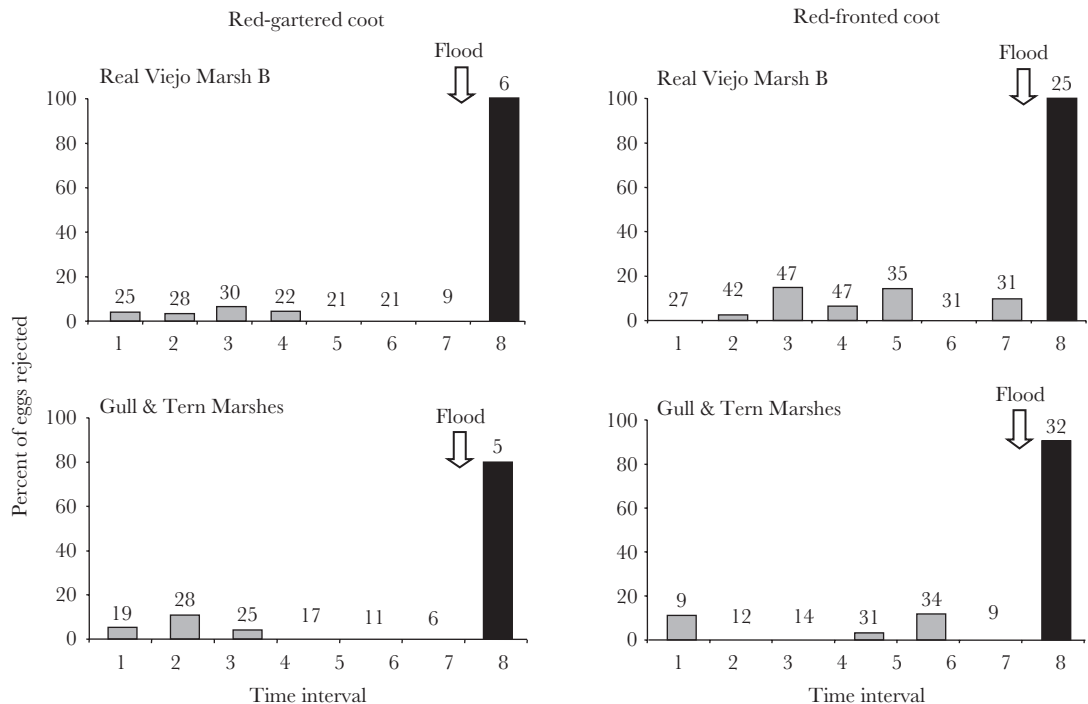


Figure 1 Rejection rates of black-headed duck eggs by the two primary hosts before and during a flood event on three wetlands in 1993. Rejection rates are for each 3–5-day time interval before and during the flood. Statistical comparisons (Table 1) contrast (a) the overall rejection rate for all pre-flood intervals combined (19 or 23 days) to rejection rates in the single interval that bracketed the flood (3 or 5 days) and (b) rejection rate for only the 6-day pre-flood interval to rejection rates in the interval that bracketed the flood (3 or 5 days). Numbers above bars are the sample size of duck eggs in nests at the beginning of each interval.

experimental parasitism with real duck eggs swapped among host nests as soon as the eggs were laid (Real Viejo Marsh B 1993), experimental parasitism with painted domestic chicken eggs whose length and width overlapped the size range of duck eggs (length: 50.5–63.5 mm, width: 41.3–47.6 mm, $n = 314$ eggs) (Cari Lauquen 1994, Real Viejo Marshes A and B 1997), and experimental parasitism with real coot eggs from nests of conspecifics (Cari Lauquen 1994, Real Viejo Marshes A). The diversity of approaches was employed originally to examine different aspects of the host–parasite interaction (e.g., Lyon and Eadie 2004, 2013) but, when the environmental changes occurred, we realized that we could leverage these experiments to evaluate how the changing environmental conditions affected rejection behavior of the hosts.

We encountered three environmental events that affected egg rejection rates, two flooding events (1993 and 1997) and a wetland that suffered a drastic loss of emergent vegetation across breeding seasons (1997). For the first flooding event (1993), we followed nests of both coot host species and, at one of the three wetlands (Marsh B), the nests included naturally parasitized nests and experimentally parasitized nests where we added real ducks that had been removed from naturally parasitized nests. For the second flooding event in 1997, natural parasitism was very rare and we used painted hen eggs to examine egg rejection rates of red-gartered coots at a single wetland, Marsh B. Finally, for the analysis of the effect of vegetation loss at Marsh A in 1997, we used painted hen eggs to assess rejection rates, but these rejection rates were compared to other wetlands and other years, some of which involved natural parasitism, while others involved experiments with painted hen eggs. We incorporated these other variables into our analysis.

In both the natural occurrences of brood parasitism and experiments with real duck eggs, parasitism occurred over a protracted period of the breeding season. We, therefore, calculated the proportion of duck eggs rejected in each time interval between visits for comparison with the single time interval that bracketed floods (Figure 1). Most wetlands were visited every 3 days, but the interval that bracketed the flood at Marsh B in 1997 was 5 days because flooding prevented access. The analysis of the data involving natural parasitism and experimental swaps with real duck eggs (Figure 1) is on a per-egg basis (proportion of duck eggs rejected) but the results are unchanged for analyses with nests as the independent data points. In the experiments with painted hen eggs, a single egg was added to each host nest in the laying or early incubation stages. Depending on year and wetland, eggs were painted white or light brown, but both colors were rejected at the same rate (Lyon and Eadie 2004). The fates of the experimental eggs were determined with as few as one or two subsequent visits, so most comparisons involve overall rejection rates during a given time period. Eggs were scored as rejected if found buried in the nest or if observed at least half buried on the final nest visit for nests that hatched or were preyed on before rejection was complete.

We used nominal logistic regression analysis to evaluate the effects of flooding, species of host, and wetland site on rejection rates of parasitic eggs in 1993. In a first set of analyses, we pooled time intervals and determined egg rejection rates for the entire time interval before the flood event and compared those with egg rejections during the interval (3–5 days) immediately after the flood. In a second set of analyses, we compared rejection rates for only the 6 days immediately before the flood to the interval (3–5 days)

immediately after the flood to ensure that any temporal patterns in egg rejection did not influence our results. We used a Fisher's exact test to contrast rejection rates before and after a second flood event in 1997 on one wetland (Real Viejo Marsh B) in an experimental study of egg rejection; this comparison involved a single wetland (Marsh B), one host species (red-gartered coots), and a single egg type (painted hen egg). We used nominal logistic regression analysis to evaluate the effects of vegetation loss, wetland site, and egg type on rejection rates of parasitic eggs. For each wetland, we pooled all egg rejections in that year.

Population impacts of reduced hatching success

We developed a simple deterministic population model to examine the influence of egg rejection rates on the reproductive success of black-headed ducks. We emphasize that the goal of this modeling exercise was simply to illustrate how variation in different vital rates might impact the demography of this poorly studied species. We did not attempt to develop a sophisticated stochastic population projection model because many vital rates and their variances are too poorly known for black-headed ducks to enable a robust analysis, and we felt it would be stretching the limits of existing data to attempt to do so. Moreover, our goal was simply to explore the demographic consequences of different combinations of life-history parameters rather than to undertake a formal population viability analysis. Hence, our model is meant to be heuristic and illustrative. Nonetheless, the value of such an approach is that it allows an initial exploration of key vital rates and serves to illustrate how even small changes in some of these parameters could have important demographic implications for the duck. Further refinement of a robust population model will await future detailed field studies, although our initial prototype can help identify which vital rates may be of particular interest and are most in need of further study.

To keep the model simple, we considered only females and assumed a closed population (no immigration or emigration and all surviving ducklings show natal philopatry), all females reproduce and start breeding at 1 year of age, and no age-specific differences in fecundity or survival. Since there are very few life-history data for this species, we used general estimates of duckling survival (0.30) and adult survival (0.60) for a typical anatid (reviews in Johnson et al. 1992; Sargeant and Raveling 1992), but we also explored variation in these parameter estimates. The number of eggs that a female black-headed duck can lay is unknown and is of particular interest given theoretical predictions of increased fecundity for an obligate brood parasite (Lyon and Eadie 1991), and so we varied this systematically as well. We assumed that a constant fraction of accepted eggs hatched; with this, hatching success is solely determined by variation in egg rejection rate. In support of this, hatching success for a given host is strongly correlated with rejection rates at the wetland level (Lyon and Eadie 2004).

The simple population equation is:

$$N_{t+1} = (N_t \cdot \phi_A) + (N_t \cdot CS \cdot (1 - \rho) \cdot \eta \cdot \sigma \cdot \phi_J \cdot \pi)$$

where N_t = number of adult females at time t (time unit is years); N_{t+1} = number of adult females at time $t+1$; ϕ_A = annual adult survival (0.60; baseline; typical for most anatids); CS = clutch size (number of eggs) laid by each breeding black-headed duck female (varied from 1 to 40 eggs; most oxyurids, the closest relatives of black-headed ducks [Livezey 1986], lay 8–10 eggs per

clutch and perhaps could lay at most three clutches in renests); ρ = rejection rate of duck eggs by hosts (0.53; baseline; from data; varied systematically from 0 to 1.00); η = proportion of eggs that hatch given that they are not rejected (kept constant in these simulations at 0.47; baseline; from data); σ = sex ratio of ducklings (assumed = 0.50 for all simulations); ϕ_J = duckling survival to age 1 after leaving nest = 0.30 (baseline; typical for most anatids; varied systematically from 0.10 to 0.50); π = natal philopatry (assumed = 1.0 for all simulations).

The parameters in the first set of parentheses represent the number of adults surviving from year N_t to year N_{t+1} , while the parameters in the second set of parentheses represent the total number of eggs that are laid, accepted, hatch, and produce surviving female recruits. We calculated population growth (λ) as a function of rejection rate, clutch size, and duckling survival.

RESULTS

Environmentally induced changes in egg rejection

During our 3-year experimental and observational study of interactions between black-headed ducks and their hosts, we discovered dramatic instability in a key aspect of the interaction. We observed several sudden, extreme increases in the rate of rejection of duck eggs by both species of coot hosts. Note that these are rates of rejection over short-term intervals and not overall rejection rates of eggs from laying to hatching. This change in host behavior was associated with two types of environmental perturbation: flooding and loss of vegetative nesting cover. In 1993, normal levels of egg rejection ranged from 0% to 20% over 3–4-day intervals for both host species on three different wetlands (Figure 1a–d; the two smallest wetlands are combined for sample size). A storm late in the breeding season, with 120 mm rain in 48 h, resulted in severe flooding, raising water levels by 25–35 cm. Coot hosts maintained their nests through the flood, but rejection rates of black-headed duck eggs escalated dramatically to 91% and 95% for red-gartered and red-fronted coots, respectively, during the single 5-day interval that included the flood (Figure 1a–d). The increase in egg rejection during the interval that bracketed the flood, relative to preflood levels, was exceptional for both species and on two different wetland complexes. The effect of flooding was highly significant ($P < 0.0001$), and this was true both when all time intervals prior to flooding were considered (Table 1a) and when analyses were restricted to only the 6 days immediately prior to flooding relative to the interval bracketing the flood event (Table 1b). There was a marginal difference in egg rejection levels among host species, but this was not statistically significant (Table 1). There were no differences in rejection rates among wetland sites.

This pattern was mirrored during a similar flood in November 1997 in an experimental study of egg rejection by red-gartered coots on one of these wetlands (Marsh Real Viejo B). During this flood, 75 mm rain fell in 48 h and water levels rose roughly 10 cm. In the 10-day period prior to the storm, 42.8% of 49 experimentally added eggs were rejected compared to 86.3% of the eggs that remained during the following 7-day interval that bracketed the flood (Fisher's exact $P = 0.0007$; 22 nests remained during the 7-day interval; 6 nests that were depredated during the interval are excluded). This increase in rejection was not simply a consequence of host behavior changing over the nesting period because

Table 1

Results of nominal logistic regression analyses to evaluate the effects of flooding, host species, and wetland site on rejection rates of parasitic eggs. Data are presented in Figure 1. The results shown in (a) compare egg rejections for the entire period before the flood event to egg rejections during the interval (3–5 days) that included the flood. Results shown in (b) compare rejection rates for only the 6 days immediately before the flood to the interval (3–5 days) that included the flood to ensure that any temporal patterns in egg rejection did not influence the results. Likelihood X^2 , odds ratios, and 95% confidence intervals (CIs) for odds ratios are provided contrasting during-flood to before-flood and red-fronted to red-gartered coot host species and two sets of wetlands (Cari Lauquen to Tern and Gull March pooled)

	Likelihood ratio X^2	P	df	Odds ratio	95% CI odds ratio	R^2	n
a) All days (intervals) before vs. during flood							
Whole model	144.70	<0.0001	3			0.40	274
Flood	132.0	<0.0001	1	83.58 ^a	27.4–254.6		
Host species	1.82	0.17	1	1.67 ^b	0.8–3.6		
Wetland site	2.25	0.14	1	1.76 ^c	0.8–3.7		
b) Last 6 days before vs. during flood							
Whole model	158.03	<0.0001	3			0.67	175
Flood	149.79	<0.0001	1	278.52 ^a	67.7–1146.2		
Host species	3.59	0.058	1	4.46 ^b	0.87–22.8		
Wetland site	0.44	0.51	1	1.53 ^c	0.42–5.5		

df, degrees of freedom.

^aOdds ratio for comparison of rejection rates during-flood to before-flood event.

^bOdds ratio for comparison of rejection rates by red-fronted coots to red-gartered coots.

^cOdds ratio for comparison of rejection rates at Marsh B to gull and tern marshes.

such changes were not observed during years without flooding. The cumulative rejection rate over the entire 17-day period, excluding depredated nests, was 93.0% ($n = 43$ eggs).

Changes to vegetation structure also significantly influenced egg rejection rates. In 1993, 33.3% of duck eggs ($n = 33$) were rejected at a well-vegetated wetland (Real Viejo Marsh A), a rejection rate similar to those at our other study wetlands and similar to rates observed in experimental studies of egg rejection (above). When we returned to this wetland in 1997, there was very little vegetative cover remaining (Figure 2a,b,e) but red-gartered coots nonetheless nested at reasonable densities (63 nests), enabling experiments with painted hen eggs. The cause of the vegetation loss was unknown. Coots on this open wetland rapidly rejected 82.9% of experimental eggs added to their nests ($n = 35$ eggs) within just 6 days (Figure 2f; Real Viejo A 1997) during a period of wind-induced waves that were considerably higher than on vegetated wetlands. This high rejection rate could not be attributed to peculiarities of this particular wetland nor to the possibility that 1997 was an anomalous year because rejection rates were considerably higher than those on (a) an adjacent vegetated wetland the same year (Real Viejo B 1997), (b) another vegetated marsh studied in 1994 where experimental hen eggs were also used (Cari Lauquen 1994), and (c) the same wetland in 1993 when emergent vegetation was abundant (Real Viejo A 1993; Figure 2f). Rather, the change in the rejection behavior of hosts appears to be most directly associated with the alteration in habitat structure. Nominal logistic regression analyses confirm a highly significant effect of vegetation loss ($P = 0.0011$; Table 2). There was no influence of wetland site (Table 2). As reported previously (Lyon and Eadie 2004), we found no evidence that the type of parasitic egg (natural black-headed duck or painted hen egg) influenced host rejection behavior ($P = 0.86$; Table 2). This effect extended beyond duck versus coot egg features: experimental conspecific parasitic eggs (coot) experienced a higher rejection rate at the wetland that lost its vegetation (Real Viejo A 1997; 5 of 8 eggs (62%)

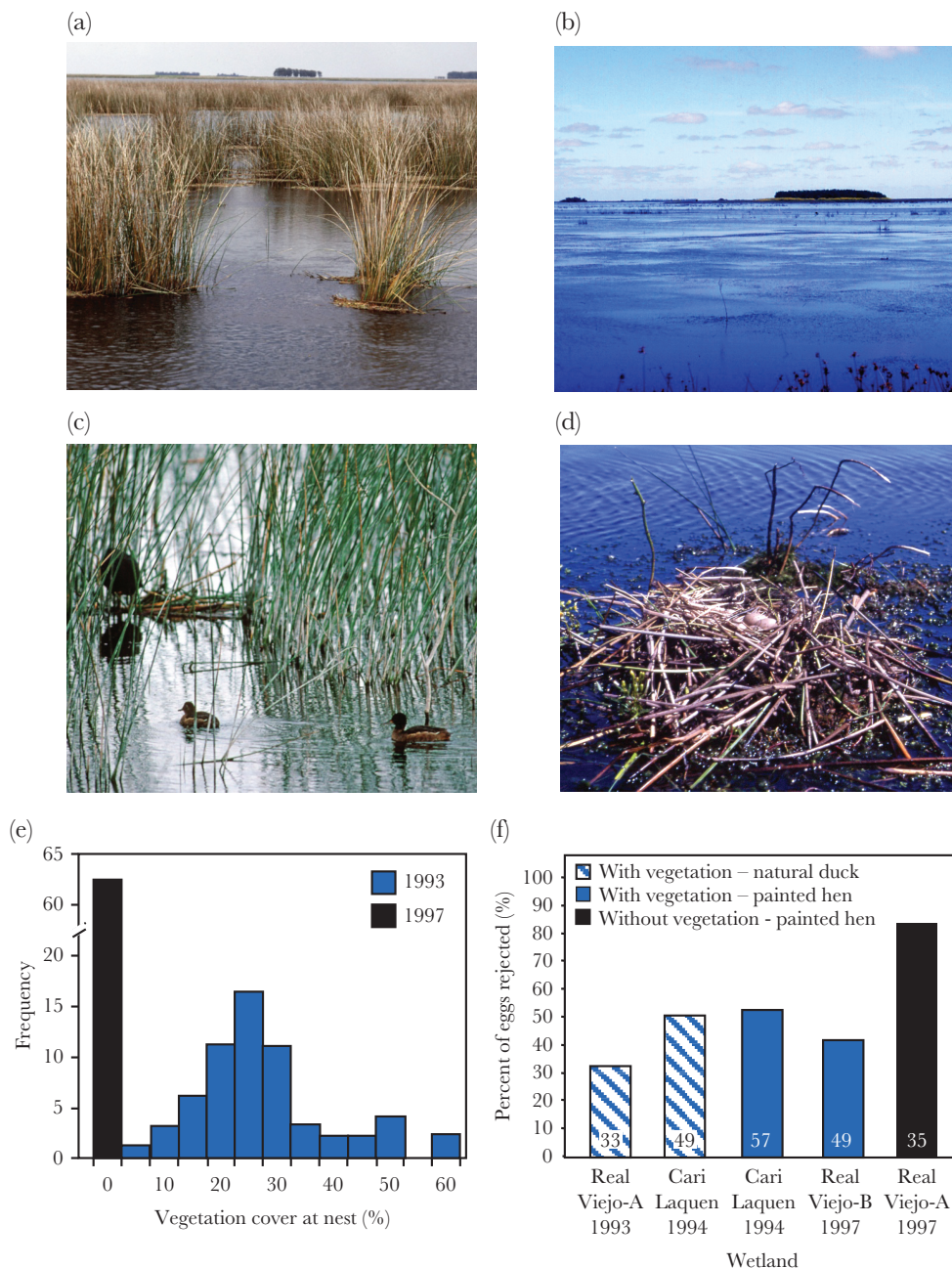
compared to a wetland with normal vegetation (Cari Lauquen 1994; 1 of 15 eggs (6%), Fisher's Exact $P = 0.0086$).

Exploring possible demographic consequences of egg rejection

The results of our simple population model to assess the potential effect of escalated egg rejection rates suggest that rejection rates of eggs >85% would be too high to maintain local populations of black-headed ducks, even if their fecundity were considerably greater than other species of waterfowl (Figure 3a). Indeed, if black-headed ducks laid a typical clutch size of 10–15 eggs common for many species of ducks, rejection rates greater than 50–60% would cause λ to fall below 1.0.

We explored other vital rates that might further exacerbate the effect of increased rejection rates. Given that black-headed duck offspring leave the host nest immediately after hatch and receive no parental care, we were especially interested in the influence of juvenile survival. Our calculations suggest that if juvenile survival rates were as high as 0.30, population growth (λ) would be positive (≥ 1.0) if females could lay more than 15 eggs (solid line in Figure 3a). However, with the rejection rates we observed during floods and on unvegetated marshes (≥ 0.90), populations would decline ($\lambda < 1.0$) even if females could lay an exceptional number of eggs (>40, dashed line in Figure 3a).

The above analysis might involve an optimistic juvenile survival rate (0.30) since it covers survival from hatch to the following year. In many species of waterfowl, duckling survival rates alone (from hatch to fledging at the age of 2–3 months) are often as low as 0.30 (Johnson et al. 1992; Sargeant and Raveling 1992; Arnold and Clark 1996) without considering over-winter mortality to the following spring. In addition, juvenile survival might be considerably lower in an obligate brood parasite where the young raise themselves without parental care. For example, if juvenile survival were more realistically 0.10, and rejection rates were those observed in our study at baseline levels (nonflooded and vegetated marshes; 0.53), population growth rates would be stable or increasing ($\lambda > 1$) only if females could lay >35 eggs. Even if black-headed ducks

**Figure 2**

The effects of vegetation loss on host rejection behavior in Real Viejo Marsh A. (a) Vegetation in 1993. (b) Marsh in 1997 after loss of vegetation. (c) Red-gartered coot nest in typical vegetated marsh with a pair of black-headed ducks in the foreground. (d) Red-gartered coot nest in 1997 in marsh after vegetation loss. (e) Frequency histogram of vegetation cover in 1993 and 1997. (f) Comparison of rejection rates of eggs by red-gartered coots in a wetland experiencing vegetation loss in 1997 (Real Viejo Marsh A) to rates in four vegetated wetlands, including the same wetland in a different year (Real Viejo Marsh A 1993), a different wetland in a different year (Cari Lauquen 1994), and a different wetland in the same year (Real Viejo Marsh B 1997; numbers at the base of the bars are sample sizes). Parasitic eggs were either natural black-headed duck eggs (hatched bars) or painted hen eggs (solid bars) as described in the methods. Statistical comparisons (Table 2) evaluate the effects of vegetation (vegetated/nonvegetated), wetland site, and egg type (natural duck eggs or painted hen eggs).

were able to lay more than 40 eggs (an extraordinary increment in fecundity for a precocial bird; Lyon and Eadie 1991), rejection rates >60% would still result in declining population growth ($\lambda < 1$; Figure 3b) and rejection rates as high as those observed in flooded conditions would reduce λ to levels that would undoubtedly ensure population instability and decline.

It is important to note that floods are irregular and so these results must be tempered by considering the frequency with which flooding

events occur. To explore this, we repeated our population simulations under different levels of flooding impact and for different values of juvenile survival using both a conservative estimate of rejection rates under flood conditions (0.80) and a higher but more typical rate based on our data (0.95; we show results using the lower rejection rate in Figure 4). Note that we measure *flood impact* as the fraction of all duck eggs laid during a year that would be exposed to flooding events, not how much of the season is under flood conditions; impact

Table 2

Nominal logistic regression analysis to evaluate the effects of vegetation loss, wetland site, and egg type on rejection rates of parasitic eggs. Data are presented in Figure 2. For each wetland, we pooled all egg rejections on that wetland in a given year. Likelihood X^2 , odds ratios, and 95% confidence intervals (CIs) for odds ratios are provided contrasting the effects of vegetation loss (nonvegetated to vegetated), wetland site (Cari Lauquen, Real Viejo Marsh A, and Real Viejo Marsh B), and egg type (painted hen eggs or natural duck eggs)

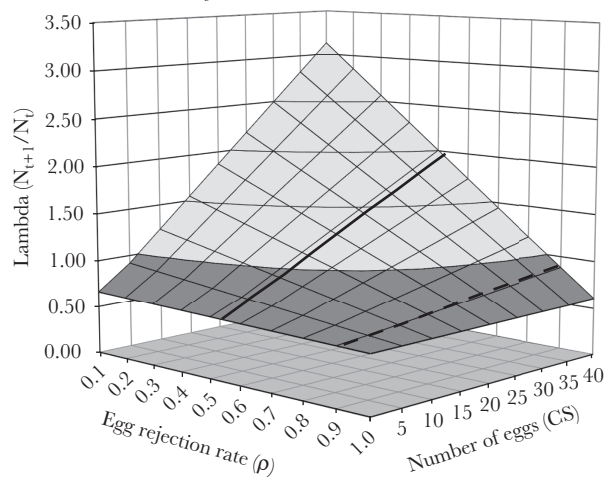
	Likelihood ratio X^2	P	df	Odds ratio	95% CI odds ratio	R^2	n
Whole model	21.01	0.0003	4			0.07	223
Vegetation loss	10.74	0.0011	1	9.06 ^a	2.3–35.7		
Wetland site	3.54	0.17	2	2.08 ^b	0.8–5.2		
Egg type	0.03	0.86	1	1.07 ^c	0.5–2.3		

^aOdds ratio for comparison of rejection rates of nonvegetated to vegetated wetlands.

^bLargest odds ratio for pairwise comparisons of rejection rates among wetlands (Cari Lauquen to Marsh A); additional pairwise odds ratios: 1.48, 0.7–3.2 CI (Cari Lauquen to Marsh B); and 1.4, 0.4–4.6 CI (Marsh B to Marsh A).

^cOdds ratio for comparison of rejection rates of painted hen eggs to natural duck eggs.

(a) Juvenile Survival (ϕ_j) = 0.30



(b) Juvenile Survival (ϕ_j) = 0.10

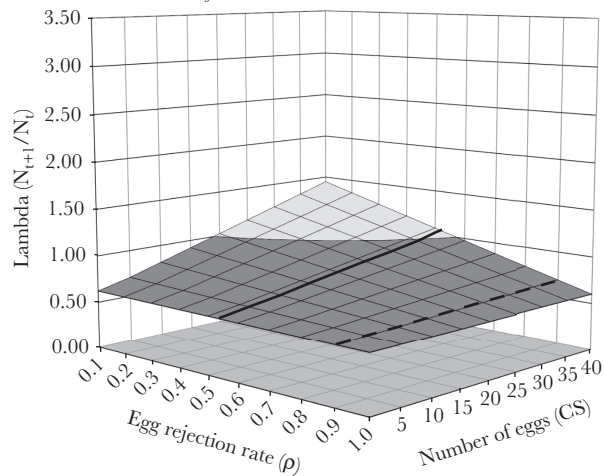


Figure 3

Demographic consequences to parasites of changes in host rejection behavior. Estimates of λ (N_{t+1}/N_t) are shown for varying combinations of parasite fecundity (CS, total number of eggs laid by parasite) and rejection rate of parasitic eggs by hosts (ρ). (a) Juvenile survival (ϕ_j) from hatch to year 1 = 0.30; (b) Juvenile survival (ϕ_j) = 0.10. Solid line indicates egg rejection rates observed before floods and in vegetated marshes (0.53, based on observed data); dashed line indicates egg rejection rates observed during periods bracketing floods and in unvegetated marshes (>0.90).

depends on when flooding occurs. For example, at peak egg season, a single short-term flood could impact 30–50% of all duck eggs. When juvenile survival is high (0.30), estimates of population growth remains positive ($\lambda > 1.0$) until the proportion of eggs subjected to flooding exceeds 70% (rejection rate = 0.80; Figure 4). With higher rejection rates (0.95), λ exceeds 1.0 only when the proportion of eggs subjected to flooding is less than 40%. Simulations using lower and more realistic estimates of juvenile survival (0.20) reveal that flood impacts as low as 10–20% could reduce λ below 1.0 (Figure 4). These results reveal the critical role of host egg rejection behavior and the interaction with juvenile survival.

DISCUSSION

The highly precocious offspring of black-headed ducks are unique among obligate parasites and their precocity has two important consequences. First, any impacts of host behavior on parasite reproductive success should be limited to the incubation stage and, second, the low costs of parasitism to hosts should result in a lack of host defenses and high parasite success in a wide variety of

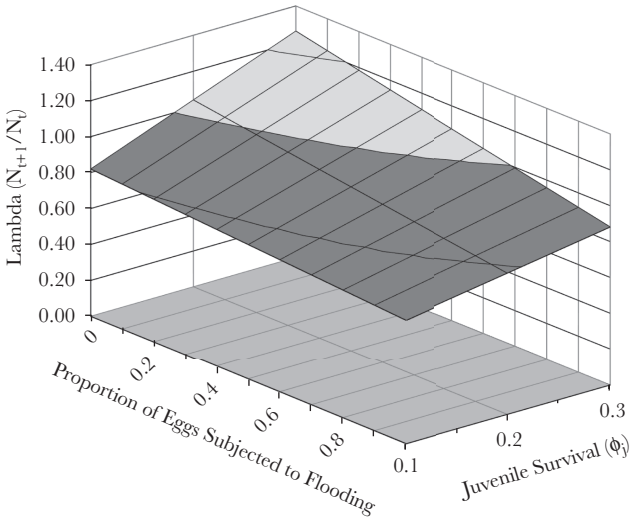


Figure 4

The effect of different flooding impacts and juvenile survival on estimates of λ (N_{t+1}/N_t). Flooding impact refers to the proportion of duck eggs in a year exposed to flooding conditions. Rejection rates during floods were modeled at 0.80. Higher rejection rates (0.95) result in even lower values of λ .

hosts. However, at our site, the black-headed duck is very specialized in terms of host use, depending mainly on two species of coots as hosts, and hatching success is low in both hosts combined (22%), mainly due to egg rejection (Lyon and Eadie 2004, 2013). Weller (1968) recorded a similar low hatching rate for one of these hosts 50 years ago at one of the sites we studied, indicating that this small margin of opportunity appears to be sufficient to allow the persistence of black-headed duck populations.

The dramatic shifts in host rejection behavior in flooded and revegetated wetlands appear to be underlain by a single behavioral mechanism, one first suggested by Weller (1968) as a possible explanation for egg rejection under normal conditions in these hosts. Coots respond to increasing water levels or large waves by building up the nest with supplemental material, raising their own eggs as the nest is augmented but leaving any black-headed duck eggs behind; the duck eggs are gradually buried as the nest is built up over them. Nests subjected to flooding and those in open water are more frequently augmented and, accordingly, rejection of black-headed duck eggs is greater in those nests.

Our observations have interesting implications for the cognitive basis of egg recognition and rejection. The extreme levels of egg rejection observed under fluctuating water levels (Figures 1 and 2) demonstrate that most, if not all, individuals of both host species have the ability to recognize parasitic eggs and could potentially reject all black-headed duck eggs. The fact that they do not do so unless faced with fluctuating water levels indicates that failure to reject duck eggs is not simply a consequence of limitations in the ability of hosts to recognize duck eggs. Rather, several lines of evidence indicate that rejection of duck eggs is an incidental byproduct of selection for conspecific egg recognition and rejection due to conspecific brood parasitism among the coots themselves (Lyon and Eadie 2004, 2013; Lyon et al. 2015). Thus, although coots can reliably distinguish their own eggs from duck eggs, and from eggs of conspecifics as well, the duck eggs apparently lack cues that trigger an “active” egg rejection response, such as outright egg ejection. Instead, duck eggs are “passively” rejected by behaviors designed to favor the host’s own eggs, such as maintaining the nest during flooding or increased wave action. The active rejection observed in hosts of other avian brood parasites, in contrast, entails behaviors that specifically target the parasitic eggs, such as direct removal from the nest by the host. Given that virtually all hosts appear capable of recognizing duck eggs, it is puzzling that they accept any duck eggs. Lyon et al. (2015) discuss several hypotheses that could explain this enigmatic pattern.

Two responses by the ducks could potentially mitigate the impacts of increased egg rejection: the evolution of egg mimicry to reduce egg rejection or a shift to parasitizing different host species. However, our previous experiments (Lyon and Eadie 2004) demonstrate that egg mimicry would not reduce egg rejection—the fine-tuned recognition that coots use to distinguish among eggs of conspecifics apparently precludes the evolution of mimicry by the ducks. Switching to new hosts is also not an option, at least on a regional scale. We exhaustively surveyed wetlands throughout the region but found no other suitable common hosts not currently parasitized (Lyon and Eadie 2013, unpublished data). Accordingly, black-headed ducks appear to be at the mercy of factors that influence egg rejection rates by their hosts, and environmentally mediated increases in egg rejection could severely impact their reproductive success.

The observation that egg rejection rates increase dramatically with changing environmental conditions has important population

and conservation implications. Black-headed ducks persist because their hosts accept and incubate some duck eggs. Hatching success rates of 20–25%—that is, those observed under normal conditions—are similar or perhaps slightly lower than the range observed for temperate nesting ducks (Johnson et al. 1992), suggesting that this level may be sufficient to maintain viable populations. However, when rejection rates exceed 90%, hatching success plummets (<10% as observed in the flooded and open marshes), lower than *almost all* published values for waterfowl generally. To evaluate this in a demographic context, we constructed a simple heuristic model to examine potential population growth rates of black-headed duck under a range of egg rejection rates and with varied assumptions of vital rates for this poorly studied species. We also explored how variation in flooding (specifically, the fraction of eggs subjected to flooding) would potentially impact duck demography. Our analyses suggest that egg acceptance rates <10% (rejection rates >90%) would be insufficient to maintain positive population growth rates, even if the fraction of eggs subjected to escalated rejection rates were relatively low (Figure 4). Moreover, this remains true even if the fecundities of black-headed ducks were considerably greater than other waterfowl species (Figure 3). We also know nothing about posthatching survival of the parasitic ducklings, but it would be remarkable if survival were equal to other species of ducks given that black-headed ducklings raise themselves without parental care. Accordingly, black-headed ducks may be persisting on very slim margins of key vital rates essential to maintain viable populations—additional environmentally driven changes in host rejection behavior could have severe consequences for reproductive success and possibly for population persistence.

We recognize that our analyses are based on a relatively small number of observed occurrences of flooding and vegetation loss. Our intent was to demonstrate simply that such environmental perturbations could have large and unforeseen behavioral and demographic consequences. Moreover, these perturbations may not be rare—they occurred in two of three years of our study (flooding in 1993 and 1997; vegetation loss in 1997). Perhaps the ducks have adapted to such dynamic systems; understanding how they do would be worthy of further study. Nonetheless, these events were sufficient to reveal that host rejection behaviors, and their impact on the ducks, can vary dramatically depending on environmental conditions, with potentially devastating consequences. The emphasis now should be to evaluate how frequently such perturbations occur and how widespread they might be. This is particularly germane given that flood and drought cycles may be further exacerbated by projected changes in global climate conditions. If El Niño-Southern Oscillation (ENSO) events become more frequent, the associated increase in flooding (Scarpati et al. 2002; Lovino et al. 2014; Barros et al. 2015) could shift the balance of host–parasite interactions against black-headed ducks. These impacts could be further exacerbated by drought, mediated by the same shift in host rejection behavior. Although we do not know what led to the massive vegetation loss observed in 1997, local ranchers told us that cattle move into marsh areas during droughts to graze on marsh vegetation. The Pampas region of Argentina is subjected to not only periods of extensive flooding but also extreme drought (Scian and Donnari 1997; Barros et al. 2015) that could lead to the loss of vegetation and further increases in egg rejection rates by hosts (whose nests are subject to wave action, requiring buildup of nests, and, consequently, rejection of duck eggs). Simply put, increases in the frequency of either drought or deluge could alter the delicate balance of host–parasite interaction with potentially dire

consequences for the parasite—the duck takes a “hit” at both ends of the environmental spectrum.

It is important to note that the dramatic reduction in the reproductive success of black-headed ducks in our study was not due to a reduced density of hosts; host densities remained high, even in 1997 when marsh vegetation was sparse. Rather, it was the behavioral dynamic between black-headed ducks and their hosts that was altered by flooding and habitat change such that coots were no longer viable hosts in flooded or open habitats. One possibility is that, in open habitats subject to vegetation loss, it may be easier for hosts to detect parasites at the nest, leading to a lowering of the threshold for rejection behavior and a concomitant increase in rejection rates as has been observed in other species (Moksnes et al. 1993; Davies and Brooke 1988; Langmore et al. 2009). However, this cannot explain the increase in rejection of black-headed duck eggs in our study because the hosts rejected experimentally added painted hen eggs rather than naturally laid duck eggs, and so hosts would not have seen an adult parasite at the nest. Interestingly, anecdotal observations suggest that the abundance of black-headed ducks declined over the 5 years of our study. The number of duck eggs per host nest dropped precipitously between 1993 and 1997 (>1.3 eggs per nest in 1993 to <0.2 eggs per nest in 1997) and surveys of other marshes within a 200-km radius of our study area indicated a similar reduction in the density of black-headed ducks in 1997. We do not know whether shifts in host rejection behavior led to this decline, but our population simulations suggest that this is a possibility.

Our observations illustrate that understanding more deeply the behavioral dynamics underlying interspecific interactions in host-parasite systems may be essential to predicting population outcomes. A new field—conservation behavior—has developed and flourished within the past two decades (Blumstein and Fernández-Juricic 2004, 2010; Berger-Tal et al. 2011), yet there are still relatively few studies that demonstrate how changes in behavioral interactions within or among species might directly impact population dynamics. Our study confirms that an understanding of the behavioral aspects of interactions between species may be critical to fully understand the effects of habitat perturbations and environmental change. Furthermore, our study highlights the need to develop a greater understanding of the demography of brood parasites. Avian brood parasites can impose substantial fitness costs to their hosts and have the potential to cause severe population impacts; accordingly, much research has focused on the consequences of parasitism to host populations. However, brood parasitism can also have important implications for the persistence and dynamics of populations of the brood parasite, but this is far less well studied. We currently lack the data to develop robust population projection models for many brood parasites, in part because of the greater challenges involved with following the full egg-laying sequences, fecundity, and survival of parasitic birds and their offspring. For this reason, our population model to explore variation in key vital rates was intentionally simple. We do not suggest that our model provides predictive population projections, nor do we intend them as such. Indeed, given the extreme levels of egg rejection observed, a model of any sort is hardly necessary to predict that the ducks may be demographically challenged. However, in the absence of better empirical data, even simple models help to illustrate potential dynamics under different scenarios and highlight critical data needs. For example, we were surprised that, using best estimates of plausible vital rates, black-headed ducks may just barely be managing to produce at a level that could maintain viable populations, even under benign conditions. Certainly, this raises a red flag that

changing environmental circumstances that escalate host rejection behavior are of concern and highlights the need for much greater emphasis on the population dynamics not only of the hosts of brood parasites but also the brood parasites themselves.

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