Original Article

Yellow warbler defenses are retained in the absence of brood parasitism but enhanced by experience with cowbirds

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Yellow warblers, *Setophaga petechia*, respond to brood parasitic brown-headed cowbirds, *Molothrus ater*, by giving "seet" alarm calls and rushing to protect their nests. These responses are typically given in populations sympatric with cowbirds, but rarely in allopatric populations. Whether the lower expression in allopatry has a genetic basis or instead could be explained by behavioral plasticity has not been investigated. We found that warblers exposed to cowbirds in Montana (sympatric) responded significantly more often to cowbird models with seet calls (85.7%) and nest protection behavior (80.0%) than conspecifics breeding in long-term isolation from cowbirds in Alaska (allopatric, 27.3% and 16.7%, respectively). Warblers breeding in Idaho, which were locally isolated from cowbirds (naive) but presumed to be genetically similar to nearby parasitized warblers, were significantly less likely than sympatric warblers to respond to cowbird models with seet calls (30.3%) and nest protection (17.3%). The lower responsiveness of naive warblers implies behavioral plasticity in trait expression, indicating that the lower responsiveness of allopatric warblers relative to sympatric warblers could be explained entirely by plasticity. The lower expression of these defenses in the absence of cowbirds may contribute to their persistence by minimizing potentially costly recognition errors.

Key words: **brood parasitism, brown-headed cowbird, coevolution, nest defense, phenotypic plasticity, relaxed selection, yellow warbler.**

INTRODUCTION

An integral component of avian parental care is defense of nests against intruders that threaten reproductive success. Nest defense can be costly because it detracts from other aspects of parental care, risks injury, and attracts predators (Montgomerie and Weatherhead 1988; Ueta 1999; Martin et al. 2000; Mutzel et al. 2013). Because of these costs, natural selection should favor discrimination that results in optimal responses toward intruders that pose varying degrees of threats (Patterson et al. 1980; Caro 2005; Campobello and Sealy 2010).

Nesting birds encounter a variety of intruders, including innocuous species that nest in the same habitat, avian brood parasites, and a diverse group of nest predators. Birds respond differently to these intruders; they often exhibit strong defensive responses toward brood parasites (Hobson and Sealy 1989; Welbergen and

Davies 2008), but generally try to lure predators away from the nest (Montgomerie and Weatherhead 1988; Gill and Sealy 1996). Although nest predation is an important source of selection for nest defense responses, the losses can be recouped with a new nesting attempt. However, brood parasitism can result in greater fitness losses because hosts may devote an entire nesting cycle to a brood with a reduced number of host young and often none at all (Rothstein 1990; Peer et al. 2013). Although birds face the threat of nest predation in nearly all areas, brood parasitism varies locally and regionally (Tewksbury et al. 1998; Hauber et al. 2004). Thus, selection might favor behavioral plasticity in defensive responses exhibited toward brood parasites (Peer and Rothstein 2010; Thorogood and Davies 2013).

The yellow warbler, *Setophaga petechia*, (hereafter "warbler") is a frequent host of the brood parasitic brown-headed cowbird, *Molothrus ater* (hereafter "cowbird"). Parasitized warblers incur reproductive losses, including clutch reduction from egg removal by cowbirds (Sealy 1992), reduced hatching success (McMaster and

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Sealy 1997), and brood reduction from competition with cowbird nestlings (Lichtenstein and Sealy 1999). Warblers respond to live or model female cowbirds at their nests by uttering "seet" calls and rushing to the nest to sit tightly in the cup, and these behaviors are given less often to other avian species or nest predators (Hobson and Sealy 1989; Gill and Sealy 1996). Though other species of birds respond more intensely to adult cowbirds than to other intruders (Robertson and Norman 1976, 1977; Peer and Bollinger 1997), warblers are unique in that their seet and nest sitting responses to cowbirds differ categorically from their responses to other intruders, which include "chip" calls and distraction displays often given in an effort to lure intruders away from the nest (Gill and Sealy 2008).

Female warblers breeding in long-term isolation from cowbirds in Churchill, Manitoba, give seet calls and protect nests in response to cowbird models significantly less frequently than those sympatric with cowbirds at Delta Marsh, Manitoba (Briskie et al. 1992; Gill and Sealy 2004). These results provide compelling evidence that the responses are beneficial in the context of cowbird parasitism, but because it is unknown whether the defenses are fixed or plastic in their expression, it is unclear whether the lower expression in allopatric populations has a genetic basis or if it is due to a lack of exposure to cowbirds. Behavioral plasticity likely contributes to the difference because female warblers give fewer seet calls and spend less time sitting on the nest in response to cowbird models in their first breeding season than older females that were more likely to have interacted with cowbirds (Hobson and Sealy 1989). Thus, the intensity of both responses may depend on experience with cowbirds, and a lack of exposure to cowbirds may explain the absence of nest protection behavior in some individuals. However, it remains unclear whether plasticity alone could explain the low occurrence of both behaviors among warblers breeding in long-term isolation from cowbirds.

In the present study, we used taxidermic mounts of cowbirds and other avian species to test warblers breeding in long-term isolation from cowbirds in central Alaska (allopatric) and compared their responses with those of conspecifics breeding in a heavily parasitized population in western Montana (sympatric). To test for behavioral plasticity, we compared the responses of sympatric warblers with those of conspecifics breeding in a third population 90 km away in Eastern Idaho, at a site where cowbirds were rare (naive). Warblers in this naive population had little exposure to cowbirds, but were assumed to be genetically similar to surrounding parasitized populations due to gene flow. If warblers exhibit behavioral plasticity in the expression of defenses, we predicted that the expression of defenses would be higher in the sympatric population compared with the naive and allopatric populations. If the defenses are not plastic but have a fixed genetic basis, these behaviors should be expressed equally in the sympatric and naive populations, and expression of defenses in these populations should be more intense than in the allopatric population.

MATERIALS AND METHODS

Study sites

Allopatric populations

Experiments were conducted near Fairbanks, AK, in June 2001 and 2003, and at Innoko National Wildlife Refuge (NWR), AK, in June 2002, near Camp Lake (63°38′N, 158°01′W). The cowbird's range is approximately 1500 km south from Fairbanks and 2000 km from Innoko NWR. Allopatric populations were considered as 1 population in the statistical analysis.

Sympatric population

In June and July of 2004, we conducted experiments at 3 sites along a 32-km stretch of the Bitterroot River in Montana where cowbirds are abundant and warblers and other hosts are parasitized at high rates (Tewksbury et al. 1998).

Naive population

In May and June of 2005 and 2006, we carried out experiments in Eastern Idaho in the Clearwater National Forest (hereafter CNF; 46°43′N, 115°05′W). This area of forested mountains has few cowbirds (see also Wright 1999; Young and Hutto 1999). In 2005, we detected only a single male cowbird, which flew over without stopping (Kuehn et al. 2014). In 2006, we observed 1–3 males and 2–5 females, but no parasitized nests were found (2005, $N = 68$ nests; 2006, $N = 146$, for 12 host species, including 93 warbler nests; Kuehn et al. 2014). Long-term census data from the Landbird Monitoring Program (University of Montana Avian Science Center) suggest that cowbirds were absent throughout the CNF between 1994 and 2004. Cowbirds were, however, regularly found in habitats outside the forest boundary (see Kuehn et al. 2014 for further details). Cowbirds in forested regions depend on human activities and development (Rothstein et al. 1980), and the relatively low level of human activities in the CNF explains their scarcity.

We assumed that warblers nesting in the naive population were either born there or arrived from natal territories from surrounding parasitized populations, and had only bred as adults in the naive population. We base these assumptions on evidence that the initial dispersal distances from natal territories are much greater than dispersal distances between breeding seasons for most bird species (Greenwood and Harvey 1982; Paradis et al. 1998). Individuals at the naive site were separated from parasitized populations by just 45–75 km, a short distance in terms of gene flow in birds (Barrowclough 1980; Moore and Dolbeer 1989; Zink 1996).

There are 2 lineages of highly migratory warblers in eastern and western North America, which diverged approximately 69 500 years before present (ybp) and came into secondary contact after the retreat of the Wisconsin glaciation (Boulet and Gibbs 2006). There are statistically significant, but low, levels of differentiation between these populations, with the largest genetic distance occurring between warblers in Alaska and Newfoundland, and much lower levels of differentiation among regions within the eastern and western lineages (Gibbs et al. 2000). As our naive population was separated from the sympatric population by the Bitterroot Mountains, gene flow may be limited. However, there is no major mountain range between the naive and other parasitized populations 60 km away in Pierce, Idaho and beyond, and no reason to believe gene flow between these populations would be impeded. Importantly, the naive population is surrounded in all directions by parasitized populations.

Experimental procedures

Model presentations at a nest began 5 days after the first warbler egg was laid, once females had begun to incubate. We presented 1 model per day, on 3 successive days in random order. Each model belonged to one of the 3 treatments: 1) cowbird: one of the 4 adult female cowbird models (*Molothrus ater obscurus*); 2) control: one of the 5 adult models of nonthreatening control species (selected randomly from: male western meadowlark, *Sturnella neglecta*; male red-winged blackbird, *Agelaius phoeniceus*; California towhee, *Pipilo crissalis*; European starling, *Sturnus vulgaris*; or hermit thrush, *Catharus guttatus*); or 3) predator: models of loggerhead shrike, *Lanius ludovicianus*, or sharp-shinned hawk, *Accipiter striatus*.

Some control species were familiar and some novel to warblers at each site, providing a control for sites where cowbirds were novel. Hermit thrushes or similar congeners (veery, *Catharus fuscescens*; gray-cheeked thrush, *Catharus minimus*; or Swainson's thrush, *Catharus ustulatus*) were present in all populations, whereas redwinged blackbirds, European starlings, and western meadowlarks were present on or adjacent to the sympatric population. The California towhee is a novel species to warblers in all 3 populations. Loggerhead shrikes and sharp-shinned hawks prey on birds the size of warblers (Scott and Morrison 1990; Joy et al. 1994), and the latter depredates nests (Joy et al. 1994). Loggerhead shrikes have not been documented to depredate nests, but northern shrikes, *Lanius excubitor*, do so regularly (Cade 1967) suggesting that both predator models were perceived as a threat. The sharp-shinned hawk model was only used for predator model presentations in the allopatric population, and this hawk was detected occasionally there. The range of the loggerhead shrike did not overlap with any sites, but northern shrikes, nearly identical in appearance, bred where the allopatric population occurred. Indeed, warblers responded in the same manner to these predators as they have in previous studies (see below) indicating that our use of this model was appropriate.

Experiments were conducted between 0600 and 1400h, and different treatments at each nest were conducted at approximately the same time each day (±30 min). We placed models 10–50 cm from nests, using the same position for all models at each nest, and made observations 5–15 m away. We limited experiments to 1 min to minimize habituation. Experiments began when an adult warbler was judged to have seen the model, based on our perception of a clear line of sight between the bird and the model, or noticeable changes in the bird's behavior (e.g., onset of rapid chipping, dramatic change in posture). During each 1-min trial, we recorded the number of seet calls female warblers gave and whether they returned to the nest (perched on the rim or sat in the cup).

The short duration and presentation of models on successive days were done to minimize "carry-over" effects observed when models are presented on the same day (Gill and Sealy 2008). We avoided testing the same individual within a breeding season. Birds were not banded, but the identification of subsequent nesting attempts was aided by the small territory sizes, the timing of new nesting attempts relative to failed attempts, and the fact that renesting warblers used material from their previous nest. To minimize the testing of the same birds between years, experiments were conducted at least 1 km from where experiments were conducted in a previous season.

Statistical analyses

To determine if variations in warbler responses differed among populations, we developed a series of generalized linear mixed models. Responses investigated were 1) probability of seet calls, 2) probability of returning to their nest (nest protection behavior), and 3) the intensity (number) of seet calls within 1 min of exposure to the treatment (cowbird, control, and predator). We fit models for each response to compare differences across the populations as a function of the different treatments. We fit the probability of seet calls and returning to the nest to binary models. The number of seet calls was fit to a zero inflated Poisson and negative binomial distributions. For all models, we used a random variable for each individual female nest-owner to account for the lack of independence of responses from individual nests and used 5 reference categories (cowbird, sympatric, sympatric/cowbird, sympatric/control, and sympatric/predator) to aid in our comparisons. To determine if differences in responses were solely a function of the variation among the populations or the treatments or if variation across the treatments changed with the different populations, we compared additive (response = population + treatment) and interactive models (response = population × treatment) using Akaike's information criterion (AIC) and a likelihood ratio test (Bolker et al. 2009). From the best models, we compared differences in the predictors using Wald's z test and investigated the 95% confidence intervals of β estimates to determine if they overlapped with the reference category. We conducted our analysis using the lme4 (Bates et al. 2012) and glmmADMB packages in R 2.14.1 (R Development Core Team 2011).

We predicted a priori that if any differences in responsiveness to cowbirds existed, sympatric warblers would be most responsive, followed by naive warblers, and then allopatric warblers (see also Kuehn et al. 2014). Additionally, to ensure that our results were not influenced by model presentation order, we added a categorical variable of presentation order to our best models to see if it improved the model fit. We compared the models using AIC.

RESULTS

Differences in all 3 responses (probability of seet calls, probability of returning to their nest, and the intensity of seet calls) were best explained by interactive models with responses varying by treatment as a function of the different populations (Table 1). Specifically, when presented with cowbird models, female warblers in the sympatric population nearly always responded with seet calls and by rushing to their nests, whereas significantly fewer allopatric

Table 1

Comparison of additive and interactive models of yellow warbler responses (probability of seet calls [seet], probability of returning to their nest [to nest], and the number of seet calls within 1 min) to different treatments (cowbird, control, and predator) across 3 populations (allopatric, sympatric, and naive)

Response	Model	df	Log likelihood	AIC	X^2	P
Seet	Additive	6	−100.46	212.9		
	Interactive	10	−83.14	186.3	34.65	<0.001
To nest	Additive	6	−118.57	249.1		
	Interactive	10	−106.37	232.7	24.40	<0.001
Number of seets	Additive	6	−383.36	782.7		
	Interactive	10	−376.49	777.0	13.75	0.008

Models were compared using log likelihoods, df, AIC, and the X^2 and P values from a likelihood ratio test of the models. AIC, Akaike's information criterion; df = degrees of freedom.

warblers responded by giving seet calls or by going to their nests (Table 2, Figure 1). Naive warblers were also significantly less likely than sympatric warblers to respond to cowbird models by giving seet calls or by going to their nests (Table 2, Figure 1). Additionally, we found the intensity of cowbird-specific behaviors also differed among populations (Table 1) with all sympatric birds making significantly more calls per minute (32.52) than when compared with all allopatric (12.41) and all naive birds (7.72). The differences in responses observed among populations (returning to the nest and seet calls) were not affected by the order in which treatments were presented. Models including a variable for the order of presentation were all >2 AIC units from the best model.

Alternatively, we found no significant difference in the probability of seet calls or the probability of returning to the nest when warblers were presented with a control model (Table 2). Nonetheless, there was evidence that fewer seet calls were given to control models by allopatric and naive warblers compared with sympatric warblers, and allopatric and naive populations also showed reductions in the number and probability of seet calls in response to predator

treatments (Table 2). Although the differences in the responses to predators were significantly different ($P < 0.05$), overlapping β estimates suggest that these relationships might not be particularly strong.

DISCUSSION

Phenotypic plasticity and persistence of cowbird-specific defenses in the allopatric population

The expression of cowbird-specific defenses (e.g., seet calls and nest protection) varied significantly among populations of warblers that differ in their current and historic levels of cowbird parasitism. Both defenses were exhibited in all 3 populations, although with greater frequency and intensity in the sympatric population relative to the naive and allopatric populations. Warblers in the naive population had little or no exposure to adult cowbirds, yet they nested only 45–60 km from warbler populations where cowbirds were abundant and are assumed to be genetically similar to parasitized warblers (e.g., Kuehn et al. 2014). Naive warblers were less likely

Table 2

Comparison of the responses (seet, return to nest, and number of calls) of sympatric female yellow warblers to allopatric and naive populations across 3 treatments (cowbird, nonthreatening species [control], and predator) using a generalized linear mixed model with the sympatric populations set as the reference categories for each treatment

Response	Treatment	Population	β	SE	Upper CI	Lower CI	z value	P
Seet (yes/no)								
	Cowbird							
		Sympatric	9.65	2.60	14.75	4.55		
		Allopatric	−19.19	3.30	−12.72	−25.66	−5.81	<0.001
		Naive	−18.71	3.41	−12.03	−25.39	−5.48	<0.001
	Control							
		Sympatric	−9.84	2.58	−4.78	−14.90		
		Allopatric	−5.30	3.93	2.40	−13.00	−1.35	0.177
		Naive	−5.87	3.69	1.36	−13.10	−1.59	0.111
	Predator							
		Sympatric	−10.13	2.75	−4.74	−15.52		
		Allopatric	−15.63	5.48	−4.89	−26.37	−2.64	0.008
		Naive	−15.44	5.74	−4.19	−26.69	−2.69	0.007
To nest (yes/no)								
	Cowbird							
		Sympatric	6.04	1.43	8.84	3.24		
		Allopatric	−13.37	2.23	−9.00	−17.74	−5.99	<0.001
		Naive	−13.12	2.40	−8.42	−17.82	−5.48	<0.001
	Control				0.00	0.00		
		Sympatric	−6.36	1.40	−3.62	−9.10		
		Allopatric	−4.53	2.61	0.59	−9.65	−1.74	0.082
		Naive	−2.47	2.08	1.60	−6.54	−1.2	0.234
	Predator							
		Sympatric	−9.19	2.67	−3.96	−14.42		
		Allopatric	−8.76	4.28	−0.37	−17.15	−2.05	0.041
		Naive	−6.93	4.35	1.60	−15.46	−1.59	0.111
Number of seet calls								
	Cowbird							
		Sympatric	3.38	1.32	5.97	0.79		
		Allopatric	−8.16	1.56	−5.10	−11.22	−5.23	<0.001
		Naive	−7.03	1.79	−3.52	−10.54	−3.93	<0.001
	Control							
		Sympatric	−1.97	1.42	0.81	−4.75		
		Allopatric	−4.17	1.67	−0.90	−7.44	−2.5	0.012
		Naive	−3.84	1.88	−0.16	−7.52	−2.04	0.041
	Predator							
		Sympatric	−2.52	1.50	0.42	−5.46		
		Allopatric	−7.97	2.13	−3.80	−12.14	−3.75	<0.001
		Naive	−6.20	2.40	−1.50	−10.90	2.58	0.010

Model output includes β estimates and upper and lower 95% CI, in addition to z values and P values from Wald's z test. CI, confidence interval; SE, standard error.
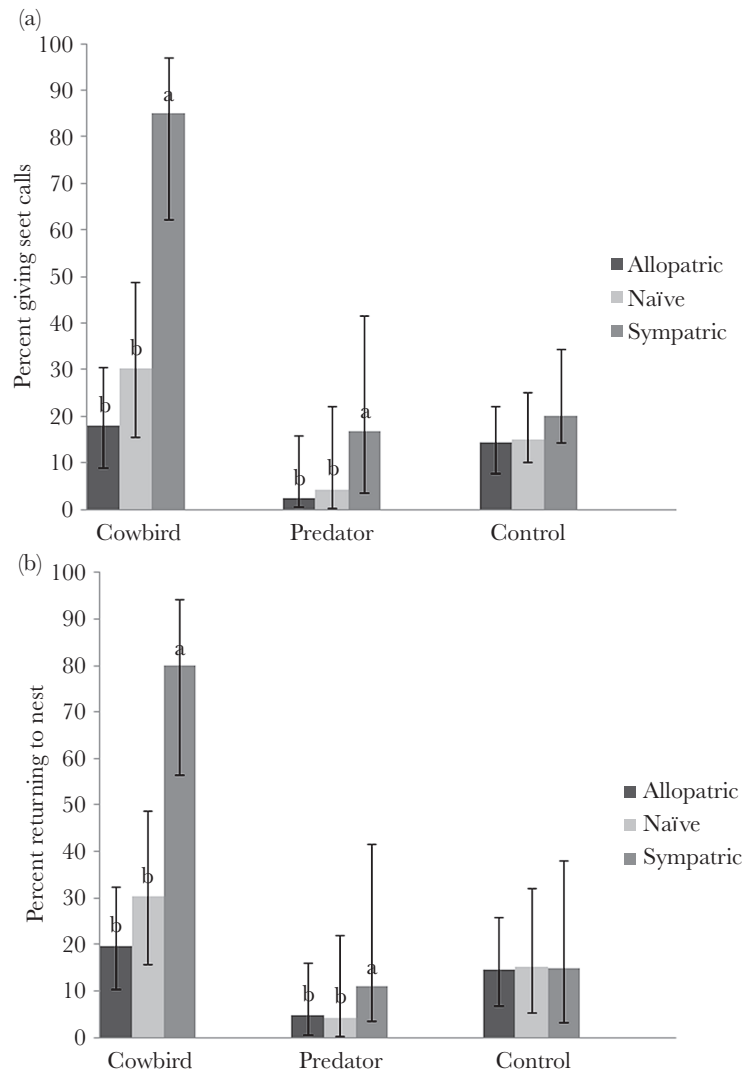
Figure 1

Percentage and 95% confidence intervals of female warblers (a) giving seet calls and (b) returning to their nests during 1-min trials involving cowbird, control, or predator models in populations exposed to cowbird parasitism (sympatric—gray), in long-term allopatry from cowbirds (allopatric—dark gray), and within the range of the cowbird but locally free from parasitism (naive—light gray). Values for bars with different letters differed significantly.

to give seet calls and return to their nests in response to cowbird models than warblers breeding 90 km away in the sympatric population, and they also gave significantly fewer seet calls to cowbird models compared with sympatric warblers (Table 1). These results suggest that seet calls and nest protection behavior are not fixed but instead are plastic traits that depend on exposure to cowbirds for their full development and expression.

Our results indicating an effect of experience agree with those of Hobson and Sealy (1989) who found that warblers in a population sympatric with cowbirds gave fewer seet calls and were less likely to return to their nests in response to cowbird models during their first breeding season compared with older individuals. More recently, Campobello and Sealy (2011) provided additional support for a learned component when they found that warblers sympatric with cowbirds increased seet calling rates after simulated trials of female cowbirds removing eggs from their nests. Their study experimentally demonstrated that the increase in seet calling rates was due to individual experience with cowbirds and not to social learning

through exposure to conspecifics interacting with cowbirds. In contrast to these studies, we found that seet calls and nest protection were not expressed by a significant proportion of naive birds when first exposed to cowbird models. For this reason, the low expression of defenses by warblers in our naive population was likely due to their lack of prior exposure to cowbirds.

Approximately one-third of warblers in the allopatric population expressed both behaviors despite long-term isolation from cowbirds and their responsiveness to cowbird models was similar to that of naive warblers. Allopatric warblers responded to cowbird models less frequently with seet calls or by returning to the nest compared with sympatric warblers (Table 1), and gave fewer seet calls to cowbirds than sympatric warblers (Table 1). Briskie et al. (1992) and Gill and Sealy (2004) found similar results when they tested warblers breeding in long-term isolation from cowbirds in Churchill, Manitoba, where warblers rarely gave seet calls and nest protection behavior in response to cowbird models (Briskie et al. 1992; Gill and Sealy 2004). Our results from the naive population discussed

above indicate that the basis for the lower expression of defenses in allopatric populations, compared with sympatric populations, need not be genetic and can instead be explained entirely by behavioral plasticity.

The widespread persistence of these defenses in warbler populations that have bred apart from cowbirds for long periods of time could be due to gene flow from parasitized populations. But this seems unlikely because the nearest parasitized populations were >1500 km away. Boulet and Gibbs (2006) showed that there was a negative, but insignificant, association between immigration and distance in the western lineage of North American warblers, and this type of relationship occurs when genetic drift has a greater effect than gene flow. It is more likely that allopatric warblers inherited the defenses from ancestors that were parasitized in the past, and the defenses have persisted under relaxed selection because they impose little or no fitness costs (e.g., Peer et al. 2007; Peer, Kuehn, et al. 2011; Peer, McIntosh, Kuehn, et al. 2011). Warblers expanded their range into northern Canada and central Alaska approximately 6300 ybp and are descendants of ancestors that bred in ice-free regions of the United States during the late Pleistocene (Boulet and Gibbs 2006). These ancestors were probably parasitized because cowbirds have been in North America at least 1 million year (Rothstein et al. 2002), and fossil evidence suggests that cowbirds ranged throughout unglaciated regions of North America during the Pleistocene in association with ungulates, which were more abundant during this period (Rothstein and Peer 2005; Peer et al. 2013). If these defenses were inherited from parasitized ancestors, our results indicate that they may have persisted for thousands of years in isolation from cowbirds, despite the opportunity for genetic drift or selection to contribute to their decay (see Kuehn et al. 2014).

Implications for trait evolution under relaxed selection

Traits that no longer provide fitness benefits are often assumed to decline when the selection pressures that favor them are relaxed, either as a result of genetic drift or because costs associated with their maintenance result in selection against their expression (Lahti et al. 2009; Kuehn et al. 2014). Because contextually dependent behavioral traits impose little cost to maintain, the strength of selection against such behaviors under relaxed selection should be dependent on the probability of recognition errors and the magnitude of the costs associated with such errors.

The specificity of the warbler seet calling and nest protection to cowbird models indicates that these responses are beneficial in the context of cowbird parasitism and that their expression toward other species represents recognition errors. Our results suggest warblers in all 3 populations occasionally make recognition errors by giving seet calls or returning to nests in response to control or predator models. In populations sympatric with cowbirds, such recognition errors may persist because the benefits of responding correctly to cowbirds outweigh any costs associated with giving them occasionally to species other than cowbirds, which could include attracting predators to the nest (Martin et al. 2000). If such costs exist and recognition errors are made regularly, selection should act against recognition errors in the absence of cowbirds, particularly in the allopatric population where cowbird-specific responses may not be optimal. But our results suggest that selection against recognition errors for these defenses has been minimal in the allopatric population. This may be due to the low nest predation rate in the allopatric population. Nests in Alaska had an 83% chance of survival from clutch initiation to fledging (Kuehn MJ, unpublished data), whereas

the nest survival rate was only 49% in the allopatric population in Churchill, Manitoba (Briskie 1995). Warblers in Alaska gave seet calls (18/66) and engaged in nest protection (17/66) significantly more often in response to cowbird models compared with warblers in Churchill (18/66 and 2/30, respectively [Briskie et al. 1992; Gill and Sealy 2004]; Fisher's Exact test, $P = 0.03; 0.01$). Although this result is consistent with the possibility that nest predation affects the retention of antiparasite behaviors, additional populations should be evaluated in this regard.

The long-term persistence of host defenses in the absence of brood parasitism supports the single-trajectory model of parasite–host coevolution (Rothstein 2001; Peer and Sealy 2004a; Peer et al. 2007; Peer, Kuehn, et al. 2011; Peer, McIntosh, Kuehn, et al. 2011) because it suggests that host communities become more resistant to brood parasitism over time as more hosts evolve and retain defenses. Other studies have shown that responses toward brood parasites are weaker in the absence of brood parasitism (Briskie et al. 1992; Gill and Sealy 2004; Langmore et al. 2012), in some cases after just several hundred years (Lahti 2005; Hale and Briskie 2007). These results could be construed as support for the coevolutionary-cycles model of coevolution (Rothstein 1990) because parasites could cycle between vulnerable hosts and well-defended hosts. However, our results confirm that lower expression of defenses in the absence of a brood parasite can be attributed largely to phenotypic plasticity, and along with other studies (Hobson and Villard 1998; Lindholm and Thomas 2000; Burhans et al. 2001), indicates that nest defense is often experience dependent. In such cases, renewed parasitism in populations that showed low defense levels would be predicted to lead to a rapid increase in resistance of hosts. Studies of other species have shown that populations descended from historically parasitized lineages retain high levels of egg rejection in the absence of brood parasites (Rothstein 2001; Peer et al. 2007; Peer, Kuehn, et al. 2011; Peer, McIntosh, Kuehn, et al. 2011) and they too would be well protected if they were to again become exposed to parasitism. Even allopatric host populations that exhibit reduced egg rejection responses, which are not plastic (Kuehn et al. 2014), would respond rapidly if they suddenly became exposed to parasitism because they still retain moderate to high levels of egg rejection behavior on which selection may act.

Yellow warblers have evolved a series of antiparasite adaptations making them unique cowbird hosts and even more exceptional when compared with other members of the warbler clade, most of whom show no adaptive response to parasitism (Peer and Sealy 2004b). In addition to having evolved specific calls to denote cowbirds and sitting in nests to prevent parasitism (Hobson and Sealy 1989; Gill and Sealy 1996, 2004), yellow warblers are also the only host that routinely buries cowbird eggs in a new nest lining, thereby minimizing the costs of parasitism (Sealy 1995; Guigueno and Sealy 2011; Kuehn MJ et al. in preparation). Our study demonstrates that seet calls and nest protection behavior are experience-dependent defenses that persist in the absence of cowbird parasitism. Future studies should address whether the egg burial responses of yellow warblers follow the same pattern as these unique alarm calls and nest protection behaviors.

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