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Cowbird parasitism of Pale-headed Brush-finch *Atlapetes pallidiceps*: implications for conservation and management

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Summary

Pale-headed Brush-finch *Atlapetes pallidiceps* is a restricted-range species that is threatened with extinction due to habitat loss. The total population of 60–80 individuals achieved a reproductive output of only 0.74 young per breeding pair in 2002. Brood parasitism by Shiny Cowbird *Molothrus bonariensis* was a major factor reducing breeding success, affecting 38.5% of broods. Parasitism rates reached 50% in an ungrazed reserve, but only 14% on an adjacent grazed plot. The resulting difference in breeding success was not, however, attributable to vegetation parameters used to describe microhabitat use. Cowbird parasitism rates therefore seem to be influenced largely by factors operating at the landscape level. These may include grazing scheme, topography, humidity and host availability. It is suggested that lower species diversity and bird abundance rendered the grazed site less attractive to cowbirds. Current parasitism rates are of great conservation concern due to the low population size of Pale-headed Brush-finch, and the initiation of controlling measures is pressing. Management options described from intensive cowbird control programmes in North America are reviewed and evaluated for their applicability here. To combine the possibility of further data collection with commencement of immediate conservation action, we consider two alternative approaches. Nest monitoring and cowbird egg removal would enable the study of the distribution of parasitism in relation to landscape and vegetation variables, whereas cowbird shooting and nest monitoring might provide a larger short-term benefit to reproductive output. Habitat management, resumption of some grazing in the reserve and cowbird removal should be considered for the intermediate future.

Introduction

The endemic and Critically Endangered Pale-headed Brush-finch *Atlapetes pallidiceps* has a restricted geographic range and is currently limited to a small side valley of the Río Jubones drainage in southern Ecuador (Collar *et al.* 1992, Agreda *et al.* 1999, BirdLife International 2000). The total population is estimated at 60–80 individuals (Krabbe 2004). While habitat loss from human landscape modification appears to be the main factor responsible for the limited distribution of Pale-headed Brush-finch, the absence of birds from suitable habitat within its former range indicates that other factors may have contributed to its decline (Krabbe 2004). Shiny Cowbird *Molothrus bonariensis*, an obligate brood parasite, is present in large numbers in the Rio Jubones drainage, where it prefers warm and dry habitats (N. Krabbe and F. Sornoza pers. comm.). It has been observed to parasitise Pale-headed Brush-finch, and cowbird parasitism is considered to have detrimental effects on the localised population of this species. Declines in sensitive species of limited geographic distribution elsewhere have been linked to the detrimental impact of brood parasitism by cowbirds (Brittingham and Temple 1983, DeCapita 2000, Rothstein and Cook 2000).

Cowbirds are largely associated with open forests and non-forest habitats (Coker and Capen 1995, Burhans 1997, Johnsgard 1997, Strausberger 2001) and have therefore benefited to a great extent from anthropogenic landscape modification (Rothstein and Robinson 1994, Donovan *et al.* 2000, Petit and Petit 2000, Ward and Smith 2000). The range of many cowbird species has expanded following the conversion of forest into fragmented and open habitat (Brittingham and Temple 1983, Peterjohn *et al.* 2000, Rothstein and Robinson 2000, Smith and Rothstein 2000). Shiny Cowbird is the most widespread brood parasite of South America, and has expanded its range considerably in recent decades (Fulton 1990, Baltz 1995, Cruz *et al.* 1995, Payne 1997, Kluza 1998, Marin 2000). It is a generalist brood parasite that has been recorded to parasitize 246 different species (Fraga 2002).

Cowbirds adversely affect the breeding success of their hosts through predation (McLaren and Sealy 2000), egg punctures (Massoni and Reboreda 2002), ejection of eggs and nestlings (Dearborn 1996, Wood and Bollinger 1997, Granfors *et al.* 2001) and competition between nestlings (Dearborn 1998, Lichtenstein and Sealy 1998). Parasitism rates in localities with high cowbird density can reach more than 90% (Payne 1997, Smith 1999), and severely reduce the reproductive output of host species. Songbird species newly exposed to cowbird parasitism often suffer high parasitism rates (Cruz *et al.* 1995), and the spread of cowbirds has often led to the decline or even local extinction of heavily parasitised host populations (Rothstein and Cook 2000).

Pale-headed Brush-finch was re-discovered in 1998, having been unrecorded for 30 years (Krabbe 2004). Its breeding success and the impact of cowbird parasitism have not previously been quantified. In March–July 2002 we surveyed the entire Pale-headed Brush-finch population and determined breeding success and factors affecting reproductive output. We focused our investigation on whether (1) Shiny Cowbirds parasitise a significant part of the population, and (2) whether habitat differences can account for varying breeding success between pairs. We used the results of this investigation to evaluate management schemes currently in place and propose new measures required to secure the population of Pale-headed Brush-finch.

Study area

The study area is located in the Yunguilla valley, approximately 50 km southwest of Cuenca in the upper Río Jubones drainage, province of Azuay, Ecuador (3°13′S; 79°16′W). It belongs to a moderately cool tropical area situated in a transitional zone between the arid lower Río Jubones valley and the humid upper reaches of the Andean west slope (Dercon *et al.* 1998). Mean annual precipitation, mean temperature and growing season differ strongly on a local scale depending on elevation and rain shadow. The region is intensively farmed, with corn crops and cattle pastures being the most dominant forms of land use (Dercon *et al.* 1998).

The study site, where the species was rediscovered in 1998 (Agreda *et al*. 1999), encompasses two hills of *c.* 50 ha each, ranging from 1,650–2,100 m above sea-level. One hill has been declared a reserve and has been ungrazed in recent years, whereas a population discovered subsequently on the neighbouring hill inhabits an area that is still grazed by cattle (Carlos and Sornoza 2001). Both hills feature semi-open habitats with dense arid scrub consisting mostly of composite and verbenaceous species, interspersed with grassland of old or recent pastures. Small stands of *Acacia* sp. and lauraceous trees are found in more humid parts. Fragments of semi-humid forest persist on western and southern slopes. Monocultural stands of dwarf bamboo *Chusquea* sp. form large patches of habitat in shallow depressions, ravines, and on the western slopes.

Methods

Breeding success survey

Breeding surveys were carried out from daylight to early afternoon every day from late March to early July 2002. Nests were located by following birds back to the nest (Martin and Geupel 1993). The outcome of nests was monitored by regular visits. Intervals between visits to active nests ranged from 3 to 5 days. If nests were found to be empty, the nest contents and surroundings were checked for signs of predation. Subsequently, the specific territory was observed intensively, to determine whether chicks might have fledged. Nest failure was denoted if (1) nests were destroyed and eggshells were found, (2) empty nests were found within 8 days of the last egg-stage visit, or (3) both adults could be observed for 60 consecutive minutes without feeding fledglings or returning to a nest. The last indicated failure because incubating females usually returned to the nest after 20 (± 5) minutes, and fledglings were fed at least every 25 (± 10) minutes (Oppel *et al.* in press-a). The rate of parasitism was calculated from the number of nests that were found with cowbird eggs or chicks, and from pairs that were feeding dependent cowbird fledglings.

For analysis, we defined every pair that raised at least one brush-finch fledgling throughout the season as successful. All pairs that were not recorded to have fledged at least one brush-finch offspring were labelled unsuccessful.

Habitat measurements

For every independent sighting of a Pale-headed Brush-finch, we recorded the following variables in an estimated 5 m radius circle around the perch site: grazing scheme (grazed or ungrazed), aspect, slope (1 = 0°–20°, 2 = 21°–40°, 3 = > 40°), habitat density (1 = open, 2 = semi-open, 3 = open scrub with visibility > 10 m, 4 = dense scrub with visibility 5–10 m, 5 = dense scrub with visibility < 5 m), vegetation cover (in the following categories: vines, bush, tree, herbaceous ground vegetation and grass, each assessed as 1 = 0–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, 5 = 81–100%), as well as bamboo cover (in % of total bush cover), and maximum and average vegetation height (both in cm). Independence of point records was assured by maintaining a 5-min time lag between consecutive observations of the same individual. Individuals were identified by location and subtle plumage differences between partners. Effective sample size was limited by the small population (Machlis *et al.* 1985). We sampled approximately 95% of the entire population, and no individual contributed more than 5% to the dataset.

Statistical analysis

We compared the breeding success between pairs in the grazed and ungrazed part using contingency table analysis and chi-square statistics to test whether differences were significant at $P < 0.05$.

In a second step, we investigated whether successful and unsuccessful pairs of Pale-headed Brush-finch exhibited different microhabitat use patterns in the study area. All point observation data were classified as successful or unsuccessful, and non-parametric tests (Mann–Whitney *U*-test) were used to examine differences between successful and unsuccessful points. We then applied a multivariate logistic regression, with nesting success as the dependent variable.

For this approach, multicollinearity between variables was reduced by eliminating one of a pair of variables with a Spearman's correlation coefficient of $r_s > 0.7$ (Sokal and Rohlf 1995, Fielding and Bell 1997). Backward stepwise logistic regression was then applied to the different sets of uncorrelated and less correlated variables to determine which variables significantly contributed to models that differentiated between breeding success states (Hosmer and Lemeshow 2000). We used Akaike's Information Criterion (AIC) to select the most parsimonious model that offered the highest degree of accuracy with the least variables (Burnham and Anderson 1992, Buckland *et al.* 1997). These variables were retained for the final model.

The final model was internally validated using the bootstrap procedure (Verbyla and Litvaitis 1989, Reineking and Schröder in press). We calculated receiver operating characteristic (ROC) curves to assess the predictive ability of the final model (Beck and Shultz 1986, Fielding and Bell 1997, Schröder 2002). The area under the ROC curve (AUC) in this case represents the model's ability to discriminate between nesting success and failure. A random prediction yields an AUC of 0.5, whereas AUC values > 0.7 can be regarded as acceptable, and > 0.8 as excellent (Hosmer and Lemeshow 2000).

Results

We surveyed 26 territories of Pale-headed Brush-finch. In seven territories no breeding attempt was recorded, and in three of these it could not be assessed whether a partner of the territory holder was present or not. A total of 18 nests were found, and another seven broods were recorded through the observation of adults leading dependent fledglings within their territories. Of the 25 recorded breeding attempts, 10 were successful and in total 17 fledglings were raised in the study area. This corresponded to a mean reproductive output of 0.74 young per confirmed pair, or 0.65 per territory.

Table 1. Breeding success of Pale-headed Brush-finch during the 2002 season in Yunguilla valley, Ecuador: a comparison between the ungrazed reserve and a grazed area of approximately equal size. Note that predation and parasitism rates are minimum figures only.

	Yunguilla reserve, ungrazed	Pasture, grazed
No. of pairs	14	9
Observation effort (hrs)	791	75
Breeding attempts recorded	18	7
Pairs without recorded broods	3	2
No. of nests found	16	2
Predated nests	7	0
Parasitized nests	7	1
Successful broods	4	6
Parasitized broods[a]	9	1
Brush-finch fledglings raised	5	12
Cowbird fledglings raised	7	1
Mixed broods	2	0
Reproductive output (young/pair)	0.36	1.33
Parasitism rate	50.00%	14.28%
Predation rate	43.75%	0

[a] Including two broods for which no nest was found (see text).

At least 10 broods were parasitized by Shiny Cowbird, leading to a total of eight cowbird fledglings being raised by Pale-headed Brush-finch. A maximum of two cowbird fledglings were raised per pair, but six of seven successful parasitism events yielded only one cowbird fledgling. Two nests were deserted after being parasitized, and seven nests were predated by unknown predators (Table 1). In four of these it could not be assessed whether they had been parasitized. The minimum overall parasitism rate of the entire population was therefore 38.5%, predation rate of discovered nests was 33.3%, and 16.7% of nests were abandoned or failed due to unknown causes.

The breeding success of the nine pairs in the grazed area was significantly higher than that of the 14 pairs in the ungrazed reserve ($\chi^2 = 9.04$, $df = 1$, $P < 0.001$). The mean reproductive output of Pale-headed Brush-finches in the grazed part was 1.33 young per pair, as opposed to 0.36 young per pair in the reserve (Table 1). Parasitism by Shiny Cowbird was more prevalent in the reserve, with at least 50% of all breeding attempts being parasitized.

Univariate analysis of microhabitat use as described by point observations indicated that successful pairs used points with lower grass cover and higher bush cover (Table 2). Grazing scheme was the only highly significant variable in all alternative logistic regression models. The best model retained grazing scheme, aspect (sin transformed), bamboo, vines and maximum vegetation height as explanatory variables (AIC = 982.792, $n = 746$; Table 3). Model performance was poor, and it had limited ability in classifying breeding success (AUC = 0.676, 95% confidence interval 0.636–0.718, Nagelkerke $R^2 = 0.132$).

Discussion

Pale-headed Brush-finch was exposed to considerable cowbird parasitism within the reserve. Parasitism rates found in this study were minimum figures only,

Table 2. Microhabitat use of Pale-headed Brush-finch pairs successfully raising offspring versus pairs that failed to raise offspring in the 2002 breeding season in Yunguilla valley, Ecuador. Samples are sightings of individuals (point observations); results are given as mean ± SD, *z* and *P* values from Mann–Whitney *U*-tests.

	Successful pairs ($n = 284$)	Unsuccessful pairs ($n = 462$)	z	P
Bush cover (%)	68.08 ± 25.60	64.56 ± 25.43	−1.97	0.048
Tree cover (%)	4.21 ± 11.27	4.68 ± 11.15	−1.38	0.250
Grass cover (%)	26.90 ± 27.02	32.52 ± 26.82	−1.97	0.002
Herb cover (%)	19.33 ± 16.08	18.60 ± 16.56	−1.38	0.331
Bamboo (%)	23.45 ± 30.23	21.56 ± 31.35	−3.17	0.253
Vines (1–5)	2.18 ± 1.076	2.09 ± 1.13	−0.97	0.157
Density (1–5)	3.08 ± 0.99	3.12 ± 1.08	−1.14	0.466
Maximum height (cm)	455.99 ± 171.77	464.89 ± 177.28	−1.41	0.310
Average height (cm)	277.78 ± 96.25	273.72 ± 91.95	−0.73	0.995

Table 3. Logistic regression model coefficients and standard error (SE) of habitat variables differentiating between successful and unsuccessful pairs of Pale-headed Brush-finch in Yunguilla valley, Ecuador, based on point observations ($n = 746$). AUC denotes the area under the ROC curve.

Variables	Coefficient	SE	P value
Grazing scheme	1.359	0.197	< 0.001
Bamboo (%)	0.008	0.003	0.008
Vines (1–5)	0.162	0.074	0.043
Maximum height (cm)	−0.001	0.001	0.029
Aspect (sin transformed)	0.771	0.161	< 0.001
AUC		0.676	
Nagelkerke R^2		0.132	

since nests were not monitored on a daily basis and unsuccessful parasitism attempts might have gone unnoticed. Predation rates were probably much higher in the ungrazed reserve than in the grazed area, and only slightly lower than parasitism rates. The detection of nest predation requires more intensive monitoring than applied in this study. Due to the unequal observation effort between grazed and ungrazed sites, we consider the bias too large to derive valid assumptions about nest predation rates. They will, therefore, not be discussed here. The unbalanced observation effort might also have introduced some bias in the pair estimates, since unsuccessful pairs in the grazed plot might have evaded detection. We used a conservative definition of breeding success to overcome the unbalanced observation effort. Successful pairs were easier to find than unsuccessful ones, and the latter required more observation effort to confirm their lack of success. With observation effort in the ungrazed part being roughly 10 times that in the grazed part, no successful pair would have been missed.

We assume that parasitism by Shiny Cowbird is one of the main factors contributing to the differences in breeding success. It should, however, be recognized that cowbird parasitism might have caused only 50% of failures. Moreover, parasitism and predation rates may vary significantly between years, and due to our limited study period we cannot assess the long-term mean of both rates.

Factors influencing breeding success

Cowbird parasitism of songbirds is affected by nest concealment and structural diversity of under-storey vegetation (Burhans 1997, Larison *et al.* 1998, Staab and Morrison 1999, Tewksbury *et al.* 1999, Uyehara and Whitfield 2000). Both the univariate comparisons and the multivariate logistic regression model indicated that successful and unsuccessful pairs of Pale-headed Brush-finch differed only marginally in their use of vegetation. One of the most important variables in the logistic regression was grazing scheme, which was selected in all alternative models. Probability of breeding success in the grazed part was approximately four times as high as probability of failure (Table 3). This suggests that land use had an overriding effect on nesting success that is not explained by microhabitat use of birds.

The positive relationship of vines and bamboo with the probability of breeding success (positive regression coefficients in Table 3) might be related to reduced predation rather than cowbird parasitism. Bamboo and vines are important substrates for nest placement of Pale-headed Brush-finch, and this has been hypothesized to prevent predation by small mammals (Oppel *et al.* in press-a).

Factors that operate at the landscape scale may govern the distribution of cowbirds if vegetation structure within territories is not different enough to explain elevated parasitism levels (Tewksbury *et al.* 1999, Young and Hutto 1999). Burhans (1997) suggested that cowbird habitat preferences or host choice at the landscape scale might contribute to differences in parasitism. Steep and narrow valleys (Tewksbury *et al.* 1999) as well as increased humidity (N. Krabbe pers. comm.) have been suggested to lower cowbird abundance. In Yunguilla valley, western slopes are generally steeper and more humid. Pairs using more west-facing slopes had lower breeding success according to the logistic regression model (Table 3). However, none of these nest failures could be attributed to cowbird parasitism. While the poor performance of the model requires caution when interpreting its results, the lower breeding success on west-facing slopes indicates that humidity might reduce not only cowbird abundance and parasitism rates, but also general habitat quality for Pale-headed Brush-finch.

It has been demonstrated that cowbirds choose their breeding areas with respect to a high diversity and abundance of potential hosts (Barber and Martin 1997, Evans and Gates 1997, Robinson *et al.* 1999, Tewksbury *et al.* 1999, Young and Hutto 1999). The generally lower diversity and abundance of bird species in grazed areas (Taylor 1986, Ammon and Stacey 1997, Dobkin *et al.* 1998, Goguen and Mathews 1998) might have attracted fewer cowbirds and led to lower parasitism rates and therefore higher breeding success of Pale-headed Brush-finch in the grazed area in Yunguilla valley. In turn the ungrazed reserve might have attracted larger numbers of cowbirds through a higher availability of potential hosts. The reserve is currently in a process of succession towards a structurally more diverse vegetation, which often leads to a more diverse avifauna (Dobkin *et al.* 1998), thus providing more hosts for cowbirds. Pale-headed Brush-finch might be a preferred host due to its nesting habits close to openings (Burhans 1997, Davis and Sealy 2000, Oppel *et al.* in press-a), and due to its ability to raise two fledglings.

All studies provided to support the hypotheses of Shiny Cowbird distribution relate to Brown-headed Cowbird *Molothrus ater* of North America. Even within the North American continent, cowbirds exhibit marked regional differences in host and habitat use (Hahn and Hatfield 1995), and it has to be considered that some conclusions may not be transferable to the situation with Shiny Cowbird present in the Yunguilla valley.

While the differences in cowbird parasitism between grazed and ungrazed sites are intriguing, it might be more practical from a conservation perspective to consider Pale-headed Brush-finch as one single population in the Yunguilla valley, especially since the sites are connected and population exchange is not restricted. The data presented in this paper suggest that cowbird parasitism is of great conservation concern. Smith (1999) suggested cowbird control to be justified when parasitism rates exceed 60% over 2 years. This may not be applicable for Pale-headed Brush-finch, since small and isolated populations are not self-sustaining at parasitism levels of greater than 20% (Greene *et al.* 1999). It therefore seems prudent to initiate management measures reducing the impact of cowbird parasitism.

Management options

Several different approaches have been used to control parasitism rates, or to remove cowbirds. The results of these programmes are highly variable (Rothstein and Cook 2000). The removal of large cowbird numbers at winter roosts or feeding sites has only limited applicability as a management tool, as the high mobility of cowbirds dilutes the removal effect across the landscape and numbers in breeding areas remain unchanged (Rothstein *et al.* 1987, Rothstein and Robinson 1994).

Most removal programmes in North America rely on large cage-traps as effective means of cowbird control (Hall and Rothstein 1999, Whitfield *et al.* 1999, Griffith and Griffith 2000, Rothstein and Cook 2000). Selective shooting has also been applied to remove cowbirds, but has yielded mixed results. While Eckrich *et al.* (1999) acknowledge site-specific shooting as an effective complementary tool to support landscape-scale management, shooting alone did not significantly reduce cowbird parasitism rates at a site in California (Whitfield 2000). Another option to reduce the impact of cowbird parasitism on the reproductive success of hosts is to monitor nests closely and remove cowbird eggs and chicks. While it is intrusive and requires a considerable level of skill (Griffith and Griffith 2000), nest manipulation has been demonstrated to be efficient and cost-effective, especially in remote areas where trapping is impractical (Winter and McKelvey 1999, Kus 2002).

Cowbird control has to be maintained for an infinitely long time, as cowbird populations at a regional level are not affected by most removal programmes (Hall and Rothstein 1999, Whitfield *et al.* 1999, DeCapita 2000, Hayden *et al.* 2000, Rothstein and Cook 2000). Despite often leading to reduced parasitism rates, cowbird removal has only occasionally triggered an evident increase in the target host population (Griffith and Griffith 2000), and it has been suggested that habitat quality or quantity might be more limiting than cowbird parasitism rates alone (DeCapita 2000).

Cowbird control does not eliminate the actual causes for declining populations (Hall and Rothstein 1999, Hayden *et al.* 2000, Rothstein and Cook 2000, Whitfield

2000), and alternatives such as habitat restoration should therefore be sought (DeCapita 2000, Griffith and Griffith 2000). The provision of suitable habitat that enables populations to overcome brood parasitism without constant human interference requires solid scientific baseline data (Hall and Rothstein 1999). For Pale-headed Brush-finch, the resumption of low-intensity grazing and selective logging is proposed as a measure to restore and preserve semi-open shrub habitats (Oppel *et al.* in press-b). However, due to the inherent variability of host — parasite interactions, results from a single field-season might not provide a sufficient basis for management decisions. The implementation of controlling measures is, however, pressing, given the low population size of Pale-headed Brush-finch. We consider two alternative approaches in an attempt to trade off the possibility of taking immediate action with the need to study parasitism patterns.

An intensive monitoring programme for Pale-headed Brush-finch should be carried out in the next breeding season. While variables that might explain parasitism can be recorded at parasitized and unparasitized nests, the removal of cowbird eggs and nestlings could minimize the impact of brood parasitism. This approach would enable the collection of more data on the distribution and causes of cowbird parasitism in the Yunguilla valley, and would help to increase the reproductive output of Pale-headed Brush-finch. It would, however, not reduce the impact associated with adult cowbirds removing eggs or nestlings of Pale-headed Brush-finch. The close monitoring of nests might also lead to increased predation rates (Martin and Geupel 1993). Furthermore, eggs of Shiny Cowbird and Pale-headed Brush-finch are both highly variable and show considerable overlap in colour and marking, rendering their reliable identification very difficult (Oppel *et al.* in press-a).

An alternative approach would be to take immediate action to reduce cowbird abundance and, potentially, parasitism rates. This would include selective shooting of cowbirds and the removal of tall vegetation (e.g. *Agave* spp., *Eucalyptus* spp.) that might serve as cowbird perches (Clotfelter 1998, Hauber and Russo 2000). Changes to the system will, however, limit the chance of further data collection and thus foreclose a better understanding of factors that influence cowbird parasitism. In order to enable further studies, shooting effort would need to be held constant across areas with different landscape features. This might be complicated by restricted access rights to private property. While an immediate reduction of cowbirds is likely to have some benefits for Pale-headed Brush-finch, this needs to be assessed with nest monitoring or breeding success monitoring. The disadvantages of the first approach would therefore apply to the second approach as well.

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