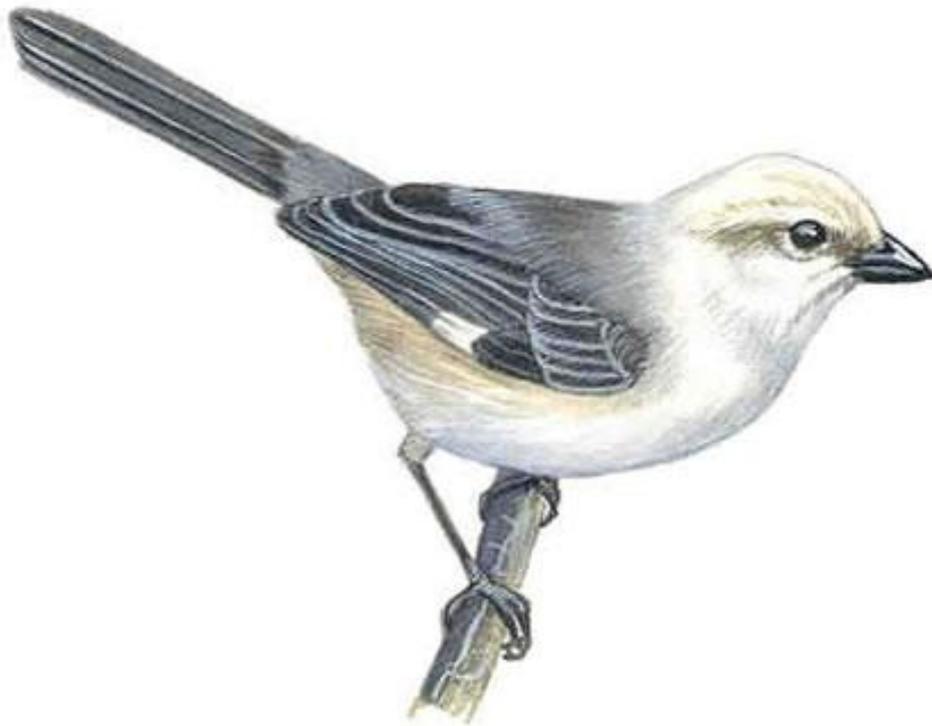


Steffen Opper

**The role of breeding biology,
habitat use, and cowbird
parasitism for the conservation
of the Pale-headed Brush-Finch
(*Atlapetes pallidiceps*) in
southern Ecuador**





Diplomarbeit

Studiengang Diplom Landschaftsökologie

Thema:

**The role of breeding biology, habitat selection,
and cowbird parasitism on the conservation of
the Pale-headed Brush-Finch in southern Ecuador**

vorgelegt von Steffen Opper

Betreuer:

Dr. B. Schröder

Prof. Dr. F. Bairlein

Oldenburg im Februar 2003

PREFACE

The world's biodiversity is decreasing at an alarming rate. Since a large proportion of the biodiversity is indigenous to tropical ecosystem, the number of species facing extinction in the tropics is substantially higher than in temperate regions. Furthermore threatened by the growth of human population and the increased pressure on remote areas for agricultural purposes, the preservation of tropical biodiversity forms one of the greatest challenges for conservationists on earth.

Many of the tropical countries have severe economic and social problems, and the importance of conservation topics is either of low priority or not acknowledged at all. The lack of financial resources and sometimes of qualified staff to propose and carry out management of natural resources renders successful conservation of biodiversity an almost insurmountable task left at the hands of the country alone.

The introduction of knowledge and resources of industrialized countries into tropical areas to support local conservation initiatives was the underlying motivation for the initiation of this project. The Pale-headed Brush-Finch is neither the most fascinating nor the most important species at threat, it is only one of many species currently experiencing the same fate. Having already been deemed extinct for 30 years, the Pale-headed Brush-Finch was "resuscitated" by its re-discovery in 1998, and a small and highly motivated group of ornithologists set about to prevent its final extinction. A reserve was purchased and a small survey was conducted, yet the lack of sufficient manpower and financial resources limited the findings and their potential to propose management objectives. With the support of a few generous donors this project could be launched to find out more about the ecological requirements of the Pale-headed Brush-Finch, and to identify the most imminent threats to its continued survival.

At first, the population size and its reproductivity had to be determined to obtain an estimate of how vulnerable the population really was. No direct breeding evidence had been presented of this bird prior to this project. In **Chapter One** I present the first description of nests, eggs, and breeding behaviour of the Pale-headed

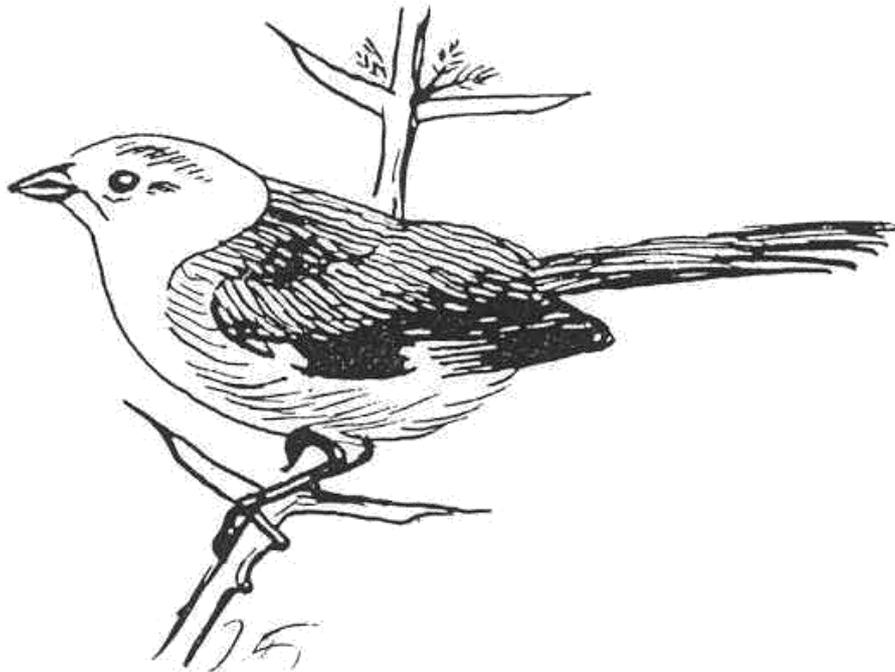
Brush-Finch, and draw a number of conclusions which are of high relevance for its future conservation.

This rather descriptive information is then followed by the main goal of the project, to reveal the habitat preferences of the Pale-headed Brush-Finch and their implications for management. Only a few quantitative descriptions on the used habitat exist, and this is complicated by the complete lack of natural vegetation in the region. What the currently most preferred habitat is, and what a natural habitat could have been, and what requirements need to be met to support the brush-finch population is examined in **Chapter Two**, based on modern analytical procedures of an extensive data set. The distribution of a species is not solely determined by its intrinsic habitat requirements, but also by the interaction with other species present at the same locality. Closely related organisms often compete with each other for natural resources, and such a competition might have negative influences on the health and viability of a population. Chapter Two is therefore not restricted to the Pale-headed Brush-Finch alone, but also quantifies the habitat requirements of the co-existing Stripe-headed Brush-Finch. Finally, the habitat use of both species is compared and conclusions are drawn as to whether interspecific competition adversely affects either of the two related species.

Interactions are not limited to closely related taxa. Predators and parasites might also play an important role in the survival of a species at a given site, and the brood parasitism by the Shiny Cowbird was discovered to exert a strong influence on the breeding success of the Pale-headed Brush-Finch. What factors enable or cause cowbird parasitism, and how large the effect of parasitism might become is discussed in **Chapter Three**. By comparing the newly found patterns of parasitism in the Pale-headed Brush-Finch to well studied systems from North America, an attempt is made to propose a management that will increase the brush-finch's survival by reducing parasitism rates.

This work might contribute a fair deal to the understanding of the resource use and the threats affecting the Pale-headed Brush-Finch. By suggesting a few management objectives I hope to improve the chances of the species' survival. Nonetheless I would like to emphasize that due to the variability of the environment a short term

study cannot resolve all the factors influencing the distribution and abundance of a species. The threat to the Pale-headed Brush-Finch is many-fold and not yet taken care of, and more research is required to assess the effectiveness of management measures and to develop more effective conservation plans. Large-scale changes in land-use, which would be necessary to provide expansive areas of suitable habitat, will likely not take place in the near to intermediate future, and it is therefore unlikely that the Pale-headed Brush-Finch will disappear from the list of endangered animals and become a common and widespread bird of the Azuay province in Ecuador.



CHAPTER ONE

FIRST DESCRIPTION OF THE NEST, EGGS AND BREEDING BEHAVIOR OF THE PALE-HEADED BRUSH-FINCH *ATLAPETES PALLIDICEPS* FROM ECUADOR

Steffen Opper

ABSTRACT - The Pale-headed Brushfinch (*Atlapetes pallidiceps*) is a critically endangered endemic bird species of Southern Ecuador. Nesting and breeding of this species were previously undescribed. Here I describe the position, size, and composition of 18 nests found during a study in Yunguilla Valley in 2002. The study area lies in a dry interandean valley and consists of a habitat mosaic of open grassland, dwarf bamboo, deciduous scrub, and secondary woodland. Most nests were placed on thin overhanging branches 1-3 m above ground, close to the foliage of dense thickets. Nesting material consisted of varying proportions of grass, twigs, and bamboo. Clutch sizes ranged from 2-3 eggs, and several nests were parasitized by Shiny Cowbirds (*Molothrus bonariensis*). Eggs were buffish-white and 24×18 mm in size. Nesting characteristics and egg measurements are generally consistent with descriptions for other *Atlapetes* species. Females alone incubated the eggs, and both partners fed the offspring. Incubation and nestling times are estimated to be two weeks each. Fledglings of the Pale-headed Brushfinch were led for eight weeks after fledging. No pair initiated a second clutch after a successful first one, but second and third clutches were recorded after nest failure had occurred. Plumage characteristics of juvenile *A. pallidiceps* are described and support the hypothesis that *A. pallidiceps* is derived from *A. leucopterus*. Additional qualitative observations of foraging behavior and singing activity are presented.

INTRODUCTION

The avian genus *Atlapetes* (Aves: Emberizinae) comprises 21 species of brush-finches which inhabit dense forest undergrowth, forest-edge or shrubby non-forest habitats in the Andes of South America (Paynter 1972, 1978; Hilty & Brown 1986; Ridgely & Greenfield 2001). Geographic differentiation and species limits are highly complex in the genus and currently under debate (Remsen & Graves 1995; Garcia-Moreno & Fjeldså 1999). The Pale-headed Brush-Finch (*Atlapetes pallidiceps*) is a critically endangered endemic of the Azuay province in southern Ecuador (Collar et al. 1992). Like several other *Atlapetes* species (Paynter 1978; Valqui & Fjeldså 1999), *A. pallidiceps* has a very restricted range that appears to be limited to the upper Rio Jubones valley system (Paynter 1972). The species was rediscovered in the Yunguilla Valley in 1998, after being unrecorded for 30 years (Agreda et al. 1999). No breeding behavior and nesting has been described so far.

The only currently known population of *A. pallidiceps* consists of approximately 30 pairs which inhabit dense secondary scrub above a semi-arid interandean valley. The area is inhabited and intensively farmed, and due to ongoing clearance of forest for the creation of pastures largely void of forest tracts (Paulsch et al. 2001). Land-use induced loss of habitat is presumed to pose a serious threat to the remnant population (Agreda et al. 1999). In March 2002, a study commenced to determine the ecological requirements of the Pale-headed Brush-Finch, and the main threats to the population, in order to derive management objectives to safeguard the species from extinction. The observations of breeding behavior and nesting are presented below.

STUDY AREA AND METHODS

The study area is located in Yunguilla Valley, approximately 50 km southwest of Cuenca in the upper Rio Jubones drainage, Province Azuay, Ecuador. It encompasses three steep (c. 45°) slopes with an area of c. 50 ha ranging from 1,650 – 2,000 m in elevation. The site

where the species was rediscovered in 1998 (Agreda et al. 1999) has been declared a reserve and is largely ungrazed, whereas a subsequently discovered population on the neighbouring hill inhabits an area that is still grazed by cattle (Carlos & Sornoza 2001). Both hills feature semi-open habitats with dense arid scrub consisting mostly of composite and verbanaceous species, interspersed with grassland of old or recent pastures. Small stands of *Acacia* and lauraceous trees are found in more humid parts, and fragments of semi-humid forest persist on western and southern slopes. Monocultural stands of *Chusquea* bamboo form large patches of habitat in small depressions, ravines or on the western slopes. The arid scrub is deciduous and sheds its leaves during the dry season from June to December, whereas the bamboo remains green all year round.

From March to July 2002 birds were monitored every morning between 05:45 and 06:45 hrs when singing activity was most prominent. Nests were searched in the centre of the male's preferred song perches and located by following birds returning to the nest (Martin & Geupel 1993). The majority of active nests was not approached closer than 3 m to minimize disturbance. Nest stage (incubation or chick feeding) was judged from parental behavior and monitored every 3-5 days. After fledging or nest failure had occurred, remaining eggs and the nest were measured and the following variables were recorded: egg length, width, and coloration, nest height above ground in a vertical line, nest diameter, depth of nest cup, circumference, material, cover. Metric variables were measured with a flexible tape measure, components of nest composition (material) were estimated to the nearest 10%, and cover was estimated by the percentage of nest shading at noon on a sunny day. Lateral cover, as described by Larison and coworkers (2001), could not be measured due to the density of vegetation.

Observations of breeding behavior were carried out at a few nest sites that were less sensitive to disturbance. Nest sites were observed for two consecutive hours during incubation, and for up to four consecutive hours during the chick feeding period, to record parental movements. Diet composition was judged mainly from food carried to the nest, and from occasional foraging observations where the prey item could be determined. Foraging behavior was recorded on an opportunistic basis whenever birds were followed.

RESULTS

Nest specifics

In total, 18 nests of 13 different pairs were found. At least another seven nesting attempts took place in which the nest could not be located. Two nests were found in each of three pairs, and three nests were found of one pair. Distances between consecutive nests of one pair ranged from 15 to 45 m.

13 nests were placed on thin (< 1cm) overhanging branches of shrubs or vines, usually close to the foliage. Five nests were found in forks or along the main stem of erect standing bushes within tall stands of grass. Height above ground ranged from 84 cm to 302 cm (Table 1). All but two nests were located on slopes exceeding 30°. The nest is a bulky open cup, constructed of small twigs, grass straws, herbaceous stems or bamboo. Moss and lichen were also integrated in the nest, but only in ornamental quantities. Depending on surrounding vegetation, material composition varied from almost entirely bamboo (90%) with a few twigs, to 70% grass, twigs, stems and no bamboo. The inside of nest cups was lined with fine grass, leaf fibers or bamboo leaves. Sizes of the nest cups are given in Table 1.

Seven nests were inspected during the incubation period, of which six contained two eggs each, and one contained three eggs. Assessment of mean clutch size was complicated by a high number of parasitic eggs of the Shiny Cowbird (*Molothrus bonariensis*) found in the nests. Cowbirds have been noted to remove host eggs when depositing their own (Wood & Bollinger 1997; McLaren & Sealy 2000; Granfors et al. 2001).

The eggs were buffish-white with a faint hinge of pink and blurred brownish flecking mainly around the thicker end. They differed markedly from cowbird eggs, which were pale bluish with dark purple spotting. Egg measurements are given in Table 2.

TABLE 1. Maximum, minimum, average values and standard deviation for selected parameters measured from *Atlapetes pallidiceps* nests in Yunguilla, Ecuador, in June 2002 (n=18).

Nest parameter	max	min	mean	SD
height above ground (cm)	302	84	184.33	61.49
outside diameter (mm)	150	100	127.22	13.09
inside diameter (mm)	85	50	69.39	8.74
depth of nest cup (mm)	60	45	50.44	4.54
circumference (mm)	510	245	384.81	64.21
cover (in /8)	8	4	5.83	1.42

TABLE 2. Maximum, minimum, average values and standard deviation for measurements of remaining eggs of *Atlapetes pallidiceps* in Yunguilla, Ecuador, in June 2002 (n=5).

Egg measurements	max	min	mean	SD
length (mm)	25	23	24	0.71
width (mm)	17	18	17.8	0.45

Breeding observations

Breeding activity commenced in February and nesting continued until late June. The first nest fledged in late March, the last nest in late June. Timing and number of clutches was highly variable between pairs. Some pairs did not start breeding until April, others that fledged their first clutch in early April did not attempt a second brood. At least two pairs initiated three nesting attempts, however only after the first two had been unsuccessful. In two pairs no signs of nesting activity were observed despite equal observation effort.

Singing activity was most prominent in the early morning hours, and continued to midday only in very humid conditions (fog, drizzle). Intensity and frequency of songs varied enormously between pairs, but generally declined during incubation and was reduced to almost zero at the nestling stage and while leading fledglings. Singing could only rarely be triggered by the use of playbacks, and even neighbouring males that intruded a given territory did not necessarily trigger a response by the territory owner. Territorial defense was weak and territory boundaries were very sketchy. In areas with high brush-finch density areas adjacent to different territories were often used by three different pairs for foraging and singing at different times. These areas did not appear to be of higher quality regarding food abundance or cover, and did probably not provide resources otherwise absent in the adjacent territories. No aggressive interactions between conspecifics, or between *A. pallidiceps* and the sympatric Stripe-headed Brush-Finch (*Buarremon torquatus*) were recorded.

Territory size ranged from approximately 0.5 to 2 hectares, and did not remain constant throughout the season. In places where a pair abandoned its territory after a failed nesting attempt, neighbouring pairs extended their home range or territories to fully occupy the vacant lot. Pairs leading fledglings often ventured into previously unvisited neighbouring areas, regardless of these areas being occupied by conspecifics or not.

The female alone appeared to build the nest and incubate, and both partners shared the task of feeding the offspring. No incubation feeding was observed. During incubation, the male approached the nest every 1-2 hours to call the female off, and both foraged together for approximately 15-20 minutes. The female returned alone and remained in dense cover and very close to the ground while approaching the nest. During the nestling stage, partners foraged independently and returned to the nest to feed the offspring every 5-25 minutes, depending on age and size of the chicks. Food items that could be identified were exclusively invertebrates, such as crickets and grasshoppers (Orthoptera), caterpillars (Lepidoptera larvae), adult Lepidoptera, beetles (Coleoptera) and earthworms (Lumbricidae). Food items were often fairly large, ranging from 1-3 cm in size. Although

adults were occasionally observed to eat fruit (*Rubus* sp.), no plant items were recorded to be fed to nestlings.

Nests were often found at the nestling stage, therefore only limited information is available regarding incubation length and fledging age of chicks. However, in three instances where the female was observed building the nest, the pair was seen with fledglings 32-35 days later, giving incubation and nestling times of approximately 12-14 days.

For the first few days after fledging the offspring remained almost stationary inside very dense thickets. Surviving fledglings were fed by their parents for at least 4-5 weeks, and some families stayed together for 8 weeks or more. No pair was observed leading more than two *Atlapetes* fledglings. Independent foraging of fledglings was observed after 3-4 weeks, but they still accepted food delivered by their parents.

In most nests that were parasitized by Shiny Cowbirds only one cowbird fledgling was raised (n=4), but two mixed broods (one cowbird, one brush-finch fledgling) and one clutch with two cowbird fledglings were also recorded. Brood parasitism affected almost half the population and is presently regarded to be the main threat to the Pale-headed Brush-Finch (Oppel unpubl. data).

Foraging behavior

Foraging was mainly recorded in scrub, only rarely were birds observed in open grassy habitat or on higher trees. Foraging heights of the birds ranged from 0 to 4 m above ground, with medium heights (2-3 m) being most frequently observed. Most prey items were gleaned from the foliage or small twigs while the bird was perched, but short sallying, hovering and flycatching were also recorded. Birds also ripped and searched through debris and dead leaves on the ground and removed prey items from the soil. Some individuals were observed to pick at inflorescences of larger bushes. Blackberries (*Rubus* sp.) were consumed regularly, and some individuals were feeding on grass seeds that could be reached from a low perch branch.

Even though bamboo scrub covered up to 75% of some territories and was used for nest sites, birds were only rarely observed to forage in bamboo. If foraging occurred in bamboo, it was usually ground foraging. No foliage-gleaning was observed in bamboo.

Plumage characteristics of juveniles

The newly fledged offspring of *A. pallidiceps* exhibits specific plumage patterns. While tail, wing and ventral coloration are almost identical to the adult plumage, the head pattern is strikingly different in being slaty gray with a prominent dark rufous to rusty-brown crown stripe. The slaty color extends to below the chin and is bordered by an off-white to buffish collar that in turn contrasts with the faintly streaked buffish-gray chest and belly. An off-white to light gray ear patch develops c. 2-3 weeks after fledging. The beak is dull yellowish horn in color with a black culmen, and bordered by two small buffy white supraloral spots. The crown stripe merges without contrast into the brown back, which differs markedly from the darker gray-brown wings. The extend of the crown stripe appears to diminish with increasing age of the juveniles. Simultaneously, the auricular patch develops stronger, giving the bird a blotchy appearance. Among the adults some birds were noted with very broad brown facial markings, others had an almost entirely white head.

DISCUSSION

The Pale-headed Brush-Finch occupies a wide variety of vegetation structures in non-forest habitats and appears to be a generalist feeder (Paynter 1972; Carlos & Sornoza 2001). Like many other *Atlapetes* species it occurs in dense thickets and shrubs in the subtropical zone in the Andes (Paynter 1978; Hilty & Brown 1986; Valqui & Fjeldså 1999; Lopez-Lanus et al. 2000; Ridgely & Greenfield 2001). Breeding appears to be closely linked to the rainy season in the area, as has also been noted for other brush-finches (Koepcke 1958; Paynter 1972). The onset of the rainy season often triggers increases in insect abundance, which might be required to compensate for elevated energetic requirements, especially nitrogen (Aguilar et al. 2000).

Nest sites were usually on steep slopes and nests were mostly found in overhanging branches or vines. The construction of nests on very thin branches or vines might reduce predation by small mammals (e.g. mustelids) which are too heavy to be supported by the small branches. The preference for steep slopes might result from this nesting preference, as overhanging branches are a more common growth form of shrubs growing on steep slopes than compared to plane areas.

Nests of other brush-finch species are generally described as open cups of straws, weeds, and grass, positioned in dense tangles close to the ground (Pereyra 1951; Paynter 1978; Hilty & Brown 1986; Greeney et al. 1998; DiGiacomo & Lopez-Lanus 2000) or higher up in trees (Salaman et al. 1998). The nest of *A. pallidiceps* conforms with these descriptions, but appears to be placed higher on average than other brush-finch nests. A potential explanation could be the co-existence with *B. torquatus*, which has been noted to displace *A. pallidiceps* from the ground (Agreda et al. 1999). *B. torquatus* nests close to or on the ground (DiGiacomo & Lopez-Lanus 2000), and the slightly elevated nest positioning of *A. pallidiceps* could potentially be a character displacement in areas of sympatric occurrence to reduce competition and nest predation rates (Martin 1996, 1998).

Nesting material is generally taken from the surroundings (c. 20-30 m) and varies accordingly with the vegetation type the nest is located in. No crucial elements could be identified and it is unlikely that *A. pallidiceps* is limited by the availability of suitable nesting material. None of the recorded behaviors or nesting characteristics differed noticeably between the grazed and the ungrazed study plots, however, due to unequal observation effort the sample size of nests found in the grazed area was very small (n=2).

Not many measurements of *Atlapetes* eggs are available in the literature, but the few described had sizes of 25×18 mm (*A. citrinellus*, Pereyra 1951) or 27.5×18.5 mm (*A. leucopis*, Salaman et al. 1998), which is similar to those of *A. pallidiceps*. Egg coloration ranges from bluish with very few or no spottings at all (Paynter 1978; Hilty & Brown 1986; Greeney et al. 1998) to pale creamy with chestnut blotches (Salaman et al. 1998). *A.*

pallidiceps eggs conform with the latter description, the bluish, heavily spotted and slightly larger eggs (25×19 mm) found in this study were ascribed to be of parasitic origin. This was based on a single observation, when a nest that was found with two buffish eggs, one bluish egg and a newly hatched chick was abandoned three days later and two buffish and two bluish eggs remained. I assumed that cowbirds might have removed the host chick and replaced it with an egg (Wood & Bollinger 1997), which led to the conclusion that cowbirds had bluish eggs. The Shiny Cowbird has been recorded to have two distinct egg-colorations, one of them being spotted and 23.6 × 18.2 mm in size (Fraga 2002). Brown-headed Cowbirds (*M. ater*) are known to have bluish eggs (Rothstein 1975).

Clutch sizes in neotropical birds are generally smaller than in temperate forest birds (Yom-Tov et al. 1994; Martin et al. 2000). Most brush-finches studied so far have clutch sizes of 1-3 eggs (Pereyra 1951; Paynter 1978; Hilty & Brown 1986; Salaman et al. 1998; DiGiacomo & Lopez-Lanus 2000), and *A. pallidiceps* fits well into this range with recorded clutch sizes of 2-3 eggs. The relatively small clutch sizes have been hypothesised to be a result of increased adult survival and reduced reproductive effort (Martin et al. 2000). This theory also predicts greater resource allocation to fewer young, which also offers an explanation to the observed single-broodedness of *A. pallidiceps*. No pair in the study area successfully raised more than one clutch in the breeding season. Second and third clutches were initiated only when the previous clutches had failed. The observation that fledglings were led by their parents for up to 8 weeks after fledging might explain the lack of second clutches after successful first ones.

In two pairs no breeding was recorded at all. This might be an artefact of low visibility due to very dense scrub and inaccessible terrain, and nests might have failed before they could be detected. However, the females of these two pairs had very strong brown markings on the head, indicating that they might have been young birds. When adult survivorship is high, it is conceivable that one year old females were not mature or experienced enough to start breeding. Alternatively, the younger birds might not have had the energetic resources to produce a second clutch after the first one had failed.

Nesting and number of produced clutches are highly dependent on external factors such as weather and food abundance and therefore vary between years. As a single breeding season cannot reliably assess the breeding strategy of a bird species, more research and especially long-term breeding data sets are required to determine the mean annual reproductive output of *A. pallidiceps*.

Paynter (1972), who pointed out the similarities of *A. pallidiceps* and *A. leucopterus*, mentioned that both species inhabit similar habitats and concluded that *A. pallidiceps* is a derivative of *A. leucopterus* that originated in the isolation of the upper Rio Jubones drainage. The currently known ranges of both species do not overlap and exhibit a complementary distribution pattern along the west slope of the Andes in Ecuador (Ridgely & Greenfield 2001). *A. pallidiceps* appears to be a larger version of the closest *A. leucopterus* population to the south (ssp. *dresseri*), and similarities have been noted even in adult plumage (Paynter 1972). Juvenile *A. pallidiceps* resemble *A. leucopterus*, which also has a slaty head with a rufous crown stripe, much more closely than conspecific adults. This supports the hypothesis that *A. pallidiceps* is a recent radiation from *A. leucopterus*. Similar to the gradually lightening head pattern of the juveniles, adults might assume an increasingly whiter head with increasing age. This could explain the variance in adult plumages observed in this study and by Paynter (1972). Partial albinism is widespread in *A. leucopterus dresseri* and adult plumages vary from dark to almost entirely white heads (Fitzpatrick 1980). This albinism might have manifested in *A. pallidiceps* to produce the generally pale-headed adults of today.

Foraging appeared to be unspecialized and a large number of different prey items were recorded. Ground foraging was less dominant than described from similar species (Paynter 1978). Insects and larvae were preferably taken, but grass seeds and flower buds were also consumed. Paynter (1972) analyzed the stomach contents of eight birds and found insect remains and cracked seeds besides large quantities of sand. The dominance of invertebrate prey observed in this study might be due to seasonal variation in food availability and consumption, as the gut analysis was carried out in November (Paynter 1972). Like most feeding generalists, other *Atlapetes* species have also been noted to be insectivorous

during the breeding season (Paynter 1978). Invertebrate prey is higher in protein and provides more energy (Bairlein 1996). Since foraging decisions of a bird tend to maximize efficiency, invertebrate prey should dominate in times with high nitrogen requirements such as the breeding season. Nestlings were fed exclusively with invertebrate prey, probably to provide more energy and nitrogen, thus enabling faster growth rates.

The fact that foraging could never be observed in bamboo scrub might be due to the monostructural composition of bamboo stands. Lower diversity in plant species and structure typically support lower numbers of invertebrates (Rotenberry & Wiens 1998; Kratochwil & Schwabe 2001; Söderström et al. 2001), which might render bamboo an inefficient foraging substrate for an unspecialized bird. On the other hand, bamboo is very dense and inhibits prolonged observations, which might have in turn led to the false assumption that it is not used for foraging.

Agreda and coworkers (1999) as well as Ridgely and Greenfield (2001) stated that pairs of *A. pallidiceps* usually forage together, which is common in several species of the genus (Paynter 1978; Lopez-Lanus et al. 2000). During the incubation period, females were guarded by their mates when leaving the nest to forage. Both during the nestling stage and while feeding fledglings, partners were often observed to forage alone. Since birds foraging by themselves do not utter contact calls which aid discovery, they are much harder to detect. I conclude that at least during the breeding season joint foraging is not more pronounced than solitary movements. This is also supported by Paynter's (1972) observations, which were mostly of single individuals and less frequently of pairs.

Territorial defense is highly variable between South American brush-finch species. D. Cadena (*pers. comm.*) noted that in a study area in Colombia *Buarremon torquatus* exhibits very strong territorial defense, whereas that of *B. brunneinucha* is much less aggressive. Agreda and coworkers (1999) stated that tape playbacks yielded only a weak response in *A. pallidiceps*. This is consistent with the results of this study, where almost no response to playbacks was recorded, and territorial defense to conspecific intruders was entirely absent at times. However, since the study did not commence until mid-March, the

time with the highest singing activity might have been missed. While the biological reason for the lack of territorial defense needs to be analyzed in more detail, this behavior is of crucial importance for the assessment of distribution and population size. Lack of singing activity has been taken as circumstantial evidence that the species was absent (Collar et al. 1992). Given the low singing intensities and the lack of response to playbacks even of breeding birds, care needs to be taken when declaring an area to be free of *A. pallidiceps*. The species is not regarded as a habitat specialist (Carlos & Sornoza 2001), and suitable habitat is still present in the surrounding area. Substantial effort needs to be made to determine whether the species is present in these areas or not. I recommend that searches should focus on the first hours of daylight in February and March when singing activity is supposed to be slightly higher (N. Krabbe and F. Sornoza, *pers. comm.*).

ACKNOWLEDGMENTS

The study was funded by the German Academic Foreign Exchange Service (DAAD), grant number 332404010, by the Sweden Club 300 and by the Royal Society for the Protection of Birds. I am grateful to F. Sornoza (Fundacion Jocotoco), H. M. Schaefer and V. Schmidt for organizing the project and granting access to the study area. C. Wickert and J. Heathcote assisted me during the nest searches. The work benefited from correspondence with N. Krabbe, D. Cadena and T. E. Martin. The manuscript was improved by helpful comments of B. Schröder, J. Dierschke, H. M. Schaefer, V. Schmidt, and F. Bairlein.

LITERATURE CITED

Agreda, A., N. Krabbe, and O. Rodriguez. 1999. Pale-headed Brushfinch *Atlapetes pallidiceps* is not extinct. *Cotinga* **11**:50-54.

- Aguilar, T. M., M. Maldonado-Coelho, and M. A. Marini. 2000. Nesting biology of the Gray-hooded Flycatcher (*Mionectes rufiventris*). *Ornitologia Neotropical* **11**:223-230.
- Bairlein, F. 1996. *Ökologie der Vögel. Physiologische Ökologie - Populationsbiologie - Vogelmenschen - Naturschutz*. Gustav Fischer, Stuttgart.
- Carlos, B., and F. Sornoza. 2001. Report on new population of *Atlappetes pallidiceps* discovered. Pages 1-3. Fundacion Jocotoco, Quito.
- Collar, N. J., L. P. Gonzaga, N. Krabbe, A. M. Nieto, L. G. Naranjo, T. A. Parker, and D. C. Wege 1992. *Threatened birds of the Americas*. International Council for Bird Preservation, Cambridge.
- DiGiacomo, A. G., and B. Lopez-Lanus. 2000. New notes on the nesting of some species of Northwestern Argentina birds. *Hornero* **15**:131-134.
- Fitzpatrick, J. W. 1980. A new race of *Atlappetes leucopterus*, with comments on widespread albinism in *A. l. dresseri* (Taczanowski). *Auk* **97**:883-887.
- Fraga, R. M. 2002. Notes on new or rarely reported Shiny Cowbird hosts from Argentina. *Journal of Field Ornithology* **73**:213-219.
- Garcia-Moreno, J., and J. Fjeldså. 1999. Re-evaluation of species limits in the genus *Atlappetes* based on mtDNA sequence data. *Ibis* **141**:199-207.
- Granfors, D. A., P. J. Pietz, and L. A. Joyal. 2001. Frequency of egg and nestling destruction by female Brown-headed Cowbirds at grassland nests. *Auk* **118**:765-769.
- Greeney, H. F., M. Lysinger, T. Walla, and J. Clark. 1998. First description of the nest and egg of the Tanager Finch (*Oreothraupis arremonops* Sclater 1855) with additional notes on behavior. *Ornitologia Neotropical* **9**:205-207.
- Hilty, S. L., and W. L. Brown 1986. *A guide to the birds of Colombia*. Princeton University Press, Princeton.
- Koepcke, M. 1958. Die Vögel des Waldes von Zarate. *Bonner Zoologische Beiträge* **9**:130-193.
- Kratochwil, A., and A. Schwabe 2001. *Ökologie der Lebensgemeinschaften - Bioökologie*. Verlag Eugen Ulmer, Stuttgart.

- Larison, B., S. A. Laymon, P. L. Williams, and T. B. Smith. 2001. Avian responses to restoration: nest site selection and reproductive success in Song Sparrows. *Auk* **118**:432-442.
- Lopez-Lanus, B., P. G. W. Salaman, T. P. Cowley, S. Arango, and L. M. Renjifo. 2000. The threatened birds of rio Toche, Cordillera Central, Colombia. *Cotinga* **14**:17-23.
- Martin, T. E. 1996. Fitness costs of resource overlap among coexisting bird species. *Nature* **380**:338-340.
- Martin, T. E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology* **79**:656-670.
- Martin, T. E., and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* **64**:507-519.
- Martin, T. E., P. R. Martin, C. R. Olson, B. J. Heidinger, and J. J. Fontaine. 2000. Parental care and clutch sizes in North and South American birds. *Science* **287**:1482-1485.
- McLaren, C. M., and S. G. Sealy. 2000. Are nest predation and brood parasitism correlated in Yellow Warblers? A test of the cowbird predation hypothesis. *Auk* **117**:1056-1060.
- Paulsch, A., R. Schneider, and K. Hartig. 2001. Land-use induced vegetation structure in a montane region of Southern Ecuador. *Die Erde* **132**:93-102.
- Paynter, R. A. 1972. Biology and evolution of the *Atlapetes schistaceus* species-group. *Bulletin Museum of Comparative Zoology* **143**:297-320.
- Paynter, R. A. 1978. Biology and evolution of the avian genus *Atlapetes*. *Bulletin Museum of Comparative Zoology* **148**:323-369.
- Pereyra, J. A. 1951. Avifauna Argentina. *Hornero* **9**:291-347.
- Remsen, J. V., and W. S. Graves. 1995. Distribution patterns and zoogeography of *Atlapetes* brush-finches (Emberizinae) of the Andes. *Auk* **112**:210-224.
- Ridgely, R. S., and P. J. Greenfield 2001. *The Birds of Ecuador - Field Guide*. Cornell University Press, New York.
- Rotenberry, J. T., and J. A. Wiens. 1998. Foraging patch selection by shrubsteppe sparrows. *Ecology* **79**:1160-1173.

- Rothstein, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. *Condor* **77**:250-271.
- Salaman, P. G. W., L. Davalos, and G. M. Kirwan. 1998. First breeding records of White-rimmed Brushfinch *Atlapetes leucopis*, with ecological notes. *Cotinga* **9**:24-26.
- Söderström, B., B. Svensson, K. Vessby, and A. Glimskär. 2001. Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape features. *Biodiversity and Conservation* **10**:1839-1863.
- Valqui, T., and J. Fjeldså. 1999. New brush-finch *Atlapetes* from Peru. *Ibis* **141**:194-198.
- Wood, D. R., and E. K. Bollinger. 1997. Egg removal by Brown-headed Cowbirds: a field test of the host incubation efficiency hypothesis. *Condor* **99**:851-857.
- Yom-Tov, Y., M. I. Christie, and G. J. Iglesias. 1994. Clutch size in passerines of southern South America. *Condor* **96**:170-177.

CHAPTER TWO

HABITAT SELECTION OF THE PALE-HEADED BRUSH-FINCH, *ATLAPETES PALLIDICEPS*, THE ROLE OF INTERSPECIFIC COMPETITION, AND IMPLICATIONS FOR MANAGEMENT

ABSTRACT – The ecological requirements of the endangered endemic Pale-headed Brush-Finch have not been quantitatively examined yet. This study analyzed the habitat selection of the Pale-headed Brush-Finch at three different spatial scales, the landscape scale, the territory scale and the nest site scale. I used compositional analysis at the landscape scale and logistic regression models at all spatial scales to determine important variables predicting the presence of the Pale-Headed Brush-Finch. To examine interspecific resource partitioning and potential competition, habitat selection by the sympatric Stripe-headed Brush-Finch was analyzed with the same methods. The Pale-headed Brush-Finch selected semi-open habitat types with intermediate scrub heights at the landscape scale, and avoided open grassland and woodland, whereas the Stripe-headed Brush-Finch chose dense and forested habitat types and avoided open and semi-open habitat. THE PALE-HEADED BRUSH-FINCH chose patches with high density and vine and herb cover within territories, and nest sites were significantly dependent on the presence of vines or bamboo. The two species had overlapping territories but differed significantly in microhabitat use, with THE PALE-HEADED BRUSH-FINCH preferring more open places with lower vegetation height, and foraging in higher vegetation strata. The theory that THE STRIPE-HEADED BRUSH-FINCH dominates over THE PALE-HEADED BRUSH-FINCH and displaces it from optimal habitat is discussed and rejected. Conclusions for the conservation of THE PALE-HEADED BRUSH-FINCH are drawn, which include the preservation of extensively grazed semi-open scrubland, and the search for new reserve sites and populations.

Keywords: *Atlapetes pallidiceps*, *Buarremon torquatus*, PALE-HEADED BRUSH-FINCH, STRIPE-HEADED BRUSH-FINCH, habitat selection, interspecific competition, conservation, logistic regression, Ecuador

INTRODUCTION

Knowledge of a species' ecological requirements is a prerequisite for successful conservation (Araujo et al. 2002; Austin et al. 1996; Luck 2002; McClean et al. 1998). The Pale-headed Brush-Finch *Atlapetes pallidiceps* (Aves: Emberizinae) is a critically endangered endemic of a semi-arid interandean valley in southwestern Ecuador (BirdLifeInternational 2000; Collar et al. 1992; Ridgely & Greenfield 2001). The total population is currently estimated to consist of approximately 30 pairs that inhabit a single valley, where the species was rediscovered in 1998, after having been unrecorded for 30 years (Agreda et al. 1999). Habitat use and preferences of *A. pallidiceps* have not been quantitatively examined yet (Carlos & Sornoza 2001; Paynter 1972; Ridgely & Greenfield 2001). In this paper, data are presented on a hierarchical habitat model of the Pale-headed Brush-Finch at three different spatial scales. We used measurements of vegetation structure and other habitat variables to create a multivariate statistical model of brush-finch habitat use. The specific objectives were to (1) determine differences between available or unoccupied areas and those used by Pale-headed Brush-Finches for territories at the landscape scale, (2) quantify usage of available habitat within each territory, (3) determine features most prominent for the selection of nest sites, and (4) use these data to discuss implications for the conservation of the Pale-headed Brush-Finch.

At the site where the only currently known population of the Pale-headed Brush-Finch exists, the Stripe-headed Brush-Finch *Buarremon torquatus* also occurs. The Stripe-headed Brush-Finch is a widely distributed bird of dense moist undergrowth and forest borders from the upper tropical to the temperate zone (Paynter 1978; Remsen & Graves 1995b; Ridgely & Greenfield 2001). Concern has been raised that this species might heavily compete with, and displace the Pale-headed Brush-Finch at its last refuge (Agreda et al. 1999). Interspecific competition has long been recognized as an important factor governing bird distributions in the Andes (Fjeldså & Krabbe 1990; Haffer 1967; Remsen & Graves 1995a, b; Terborgh & Weske 1975).

Both Paynter (1978) and Remsen and Graves (1995a; 1995b) noted that sympatrically occurring brush-finch species differ in microhabitat use to reduce interspecific competition at a given site. This behavioral character displacement has been demonstrated to be an evolutionary stable strategy in temperate forest birds (Martin 1998; Rice 1978). Remsen and Graves (1995b) could not resolve the role of interspecific competition as a determinant for distribution patterns, but noted that their mapping technique was inadequate for distinguishing between syntopy and fine differences in habitat preferences and elevation. In this study we analyzed the habitat use and small-scale distribution of both species, and tried to determine whether competitive exclusion or fine-scale differences in microhabitat use are prevalent at a site of co-existence. We then compared the measured habitat preferences with existing data to examine whether one or both species adapt to the presence of congeners by using slightly different resources.

METHODS

Study area

The study area is located in Yunguilla Valley, approximately 50 km southwest of Cuenca in the upper Rio Jubones drainage, Province 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 Rio Jubones valley and the humid upper reaches of the west slope Andes (Dercon et al. 1998). Mean annual precipitation, mean temperatures and growing season differ strongly on a local scale depending on elevation and rain shadow. The study area has an estimated growing season of 5-7 months, and 3-5 humid months with an annual rainfall of 700-1000 mm (Bossuyt et al. 1997). Confusion exists as to the natural vegetation of the area. It falls into a range of dry deciduous to evergreen woodland (Blasco et al. 2000; Schultz 1988), but other authors mention evergreen scrub, lower temperate forest and herbfields as natural vegetation (Dercon et al. 1998). Landslides and natural fires can be presumed to have been frequent natural phenomena in the area (Bussmann 2001; Paulsch & Czimczik 2001). The region is intensively farmed, with corn crops and cattle pastures being the most dominant use forms (Bossuyt et al. 1997; Dercon et al. 1998).

The study site encompasses three steep (c. 45°) slopes with an area of c. 50 ha ranging from 1650 – 2100 m in elevation. The site where the species was rediscovered in 1998 (Agreda et al. 1999) has been declared a reserve and is largely ungrazed, whereas a subsequently discovered population on the neighbouring hill inhabits an area that is still grazed by cattle (Carlos & Sornoza 2001). Both hills feature semi-open habitats with dense arid scrub consisting mostly of composite and verbanaceous species, interspersed with grassland of old or recent pastures. Small stands of *Acacia* and lauraceous trees are found in more humid parts, and fragments of semi-humid forest persist on western and southern slopes. Monocultural stands of dwarf bamboo (*Chusquea spec.*) form large patches of habitat in small depressions, ravines or on the western slopes. The arid scrub is deciduous and sheds its leaves during the dry season from June to September, whereas the bamboo remains green all year round.

Two permanent water courses run parallel to the reserve at the bottom of each slope, and small gullies in depressions on the slopes contain water during and shortly after the wet season.

Territory mapping

Birds were monitored from first daylight to early afternoon every day from late March to mid-June 2002. Territory boundaries were defined by the outermost song perches connected to form a minimum convex polygon (SOURCE??). For analysis, we assigned mutually used areas between territory centres to either of the two neighbouring pairs. Habitat features were mapped in June 2002, and structural units were defined by five variables: habitat type (1=open grassland and crops, 2=semi-open grassland with single bushes covering <50%, 3=semi-open grassland with single bushes covering >50%, 4=low deciduous scrub <4m height, 5=low bamboo scrub <4m height, 6=tall deciduous scrub >4m height, 7=tall bamboo scrub >4m height, 8=mature forest or woodland, 9=prominent solitary trees), habitat density (1=open, 2=semi-open, 3=open scrub with visibility >10m, 4=dense scrub with visibility 5-10m, 5=dense scrub with visibility <5m), ground cover by grass or herbaceous vegetation (1=0-20%, 2=21-40%, 3=41-60%, 4=61-80%, 5=81-100%), dominant type of ground vegetation (grass or herbs) and average height of the woody scrub (1= 0-2m, 2=2-4m, 3=4-6m, 4= >6m). Due to the lack of detailed topographic maps and the steep slopes we used photographs taken from the opposite slope as underlying map source. This inevitably leads to a distortion along the slope, but since we used

only relative measures of use and availability, the distortion, which was the same for territories and the habitat resource map, should have a negligible effect on our results.

Point sampling

At every independent sighting of a Pale-headed or Stripe-headed Brush-Finch we recorded the following variables in an estimated circle of 5m radius around the perch site: aspect (in °), inclination (1=0-20°, 2=21-40°, 3=>40°), bush cover (in %), tree cover (in %), grass cover (in %), cover of herbaceous ground vegetation (in %), bamboo (in % of total bush cover), maximum height of the vegetation (in cm), average height of the vegetation (in cm), and position of the bird (in cm). When more than one bird was recorded at a site, we averaged the position of the birds and used the sighting as one data set to maintain independency.

To compare resource use with availability we measured the same habitat variables at 332 points that were placed in a stratified random pattern across the study area. At each random point the potential presence or absence of *A. pallidiceps* and *B. torquatus* were also recorded, based on previous observations and the observer's knowledge of the study site. The random points that fell within known territories of a species were defined "available" to that species at the microhabitat level.

Nests of *A. pallidiceps* were located using standard searching techniques (Martin & Geupel 1993; Opper et al. in prep.), and the same variables were measured.

Model construction and statistical analysis

The comparison of used and available habitat parameters is a common method to determine habitats selected by animals (Arthur et al. 1996; Hildén 1965; Johnson 1980; Jones 2001; McClean et al. 1998; Naugle et al. 1999; Neu et al. 1974; van den Berg et al. 2001). Birds usually select habitat features at different spatial scales, necessitating scale-dependent analysis of habitat selection when modeling bird-habitat relationships (Illera 2001; Johnson 1980; Jones 2001; Luck 2002; Naugle et al. 1999; Orians & Wittenberger 1991; Wiens et al. 1987). In this study we used three spatially different approaches to determine important variables that influ-

ence habitat selection of *A. pallidiceps* at the landscape scale, the territory scale and the nest site. To compare the two sympatric brush-finch species, the habitat selection of *B. torquatus* was analysed accordingly at the landscape scale and the territory level.

To describe the use of habitat features by the Pale-headed Brush-Finch at the landscape scale, we intersected the map of all territories with a habitat feature map of the study area using ArcView GIS software (Gottschalk 1995; Sandkühler & Schröder 1999). This yielded the proportion of every variable category for both the territories (use) and the entire study area (available). We tested for departure from random use of all categories combined using chi-squared goodness-of-fit analysis (Allredge & Ratti 1986, 1990; Neu et al. 1974). Habitat selection was then examined using methods based on the log ratio differences between utilized and available habitat features. This technique overcomes the unit-sum constraint caused by the lack of independence between proportions that sum to 100% (Aebischer et al. 1993; Johnson 1980). In compositional analysis, a log-transformed ratio of one category over a random other from the same variable results in linearly independent data (Aebischer et al. 1993). The log-ratios of utilized habitat proportions are compared with the log-ratios of available habitat proportions, and the difference is zero when the category is used at random. (Aebischer et al. 1993; Johnson 1980). We computed a matrix of all log-ratio differences for every habitat category using alternate categories as denominator. The log-ratio difference for every matrix cell was calculated separately for every brush-finch territory to reduce bias from pooled data (Schooley 1994). Deviation from zero (random use) was tested using one-sample randomization test with a significance level of $P < 0.05$ (Manly 1997). Zero-values for a certain category in a given territory were replaced with 0.001 to enable calculation (Aebischer et al. 1993). The outcome of the matrix represents the relative preference of the numerator category over the denominator category. Categories can then be ranked by the sums of all log-ratio differences. The largest positive value representing the most preferred, the smallest (largest negative) value the least preferred category (Aebischer et al. 1993; Graham 2001; Ratcliffe & Crowe 2001).

The results of the area-based analysis of habitat selection at the landscape scale were compared to a logistic regression model comparing used points with random points outside *A. pallidiceps* territories (unused points). This procedure was also possible for *B. torquatus*, for which no

territory map was available. The analytical procedure of the logistic regression is described below.

Point sampling data were first tested for normality using Kolmogorov-Smirnov tests. When data were not normally distributed, and transformations to normalize the data were unsuccessful, non-parametric tests (Mann-Whitney-U-test) were used to examine differences between used and non-used points.

Microhabitat selection of *A. pallidiceps* and *B. torquatus* was analyzed at the territory level. We compared the used sites with available random sites within each species' territories by constructing logistic regression models (Hosmer & Lemeshow 2000). To obtain an accurate model with a low level of complexity, variables included in the model have to be selected carefully (Buckland et al. 1997; Burnham & Anderson; Chatfield 1995). First, 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 & Rohlf 1981). We then applied backward stepwise logistic regressions from the different sets of uncorrelated variables to determine which variables significantly contributed to models that predict the probability of occurrence (Hosmer & Lemeshow 2000). We used Akaike's Information Criterion (AIC) to choose the model that offered the highest degree of accuracy with the least variables and retained those variables for the final model (Buckland et al. 1997; Burnham & Anderson 1992; Reineking & Schröder in prep.).

All models were internally validated to assess the success of calculated predictions. One problem in use-availability study designs is that the dependent variable does not fall into mutually exclusive states (Boyce et al. 2002). Standard classification procedures like receiver-operating characteristic (ROC) curves (Beck & Shultz 1986; Henley & McNeil 1982; Zweig & Campbell 1993) are therefore inappropriate measures to assess the predictive success of a use-availability model. An alternative is to use relative frequencies of probability of occurrence classes within the presence subset of the test data to evaluate the predictive success of a model (Boyce et al. 2002). Use-availability models were therefore tested by cross-validation, using four parts of the study area as training data set and one part to classify the accuracy of the obtained model (Steyerberg et al. 2001; Verbyla & Litvaitis 1989). We applied the model obtained from 4/5 of the full data set to the remaining subset, and classified predicted probabilities into 10 score

bins. If the relative frequency of observations within a bin was positively correlated (Spearman $r_s > 0.7$) to the bin value then the model was considered accurate.

Models with mutually exclusive states of the dependent variable (use vs. non-use) were validated using bootstrapping procedures (Steyerberg et al. 2001; Verbyla & Litvaitis 1989). We calculated ROC curves to classify predictive success of the final model (Beck & Shultz 1986; Fielding & Bell 1997). ROC curves analyze the correct classifications across all possible cut-off points and are therefore more reliable measures of accuracy than simple contingency tables (Zweig & Campbell 1993). The area under the curve (AUC) represents the probability of correct classifications independent of an arbitrarily defined cut-off value (Henley & McNeil 1982).

To examine whether *A. pallidiceps* displays nest site selective behavior, we compared the habitat parameters obtained from nest sites (Oppel et al. in prep.) with non-nest random sites within those territories where nests were found. The same model selection procedures as above were applied.

Similarly, it was tested whether *A. pallidiceps* and *B. torquatus* use the same resources at the microhabitat scale. We compared all observations using univariate Mann-Whitney-U-tests, and a logistic regression was then applied using the same model selection and validation procedures as described above for use vs. non-use designs, to describe the probability of an observation belonging to the Pale-headed Brushfinch.

Statistical analysis was performed with SPSS software (SPSS Corp. 1997). Results are given as means \pm SD.

RESULTS

Landscape scale

In total, 26 territories of *A. pallidiceps* were found in the study area. The highest density of birds was on the east slope of the reserve with 12 territories partially overlapping each other. Preliminary analysis indicated that territories were not placed at random across the ten habitat

types in the study area ($\chi^2=240.42$, d.f.=18, $P < 0.001$). Semi-open habitat types covered 48.8% (± 20.7) of all territories, and scrub lower than 4 m contributed another 35% (± 16.5) to all territory areas. Open grassy areas and crops occupied only small areas in territories (1.0% coverage ± 2.0), despite being common in the study area (15% coverage). Tall scrub (>4 m) comprised 18.4% of the study area and was represented in similar proportions in territories ($15.6\% \pm 16.8$). Forest remnants covered 6.8% of the area, but were basically excluded from territories ($0.1\% \pm 0.8$). Use of average vegetation height strongly deviated from random use, with scrub heights between 2 and 4 m being consistently preferred, and vegetation lower than 2 m and higher than 6 m consistently avoided ($\chi^2=99.96$, d.f.=6, $P < 0.001$). Open country (density category 1) was used less than expected from availability ($\chi^2=31.91$, d.f.=2, $P < 0.001$), semi-open and dense scrub (categories 2 and 4) were used more than expected ($\chi^2_{\text{dens2}}=38.98$, d.f.=2, $P < 0.001$; $\chi^2_{\text{dens4}}=8.77$, d.f.=2, $P < 0.01$), and the densest and intermediate habitat patches (density 3 and 5) were used approximately at random. ($\chi^2=0.50$, d.f.=12, $P > 0.05$). Areas with ground cover between 0-40% were used more than available on average ($\chi^2=31.36$, d.f.=4, $P < 0.001$), intermediate ground cover (41-80%) was used approximately at random, and areas with high ground cover ($>80\%$) were used less than available in the study area ($\chi^2_{\text{dens4}}=6.38$, d.f.=2, $P < 0.01$). The type of ground cover, whether grass or herb, did not differ significantly between used areas and available proportions.

The ranking matrix obtained from compositional analysis ordered the habitat types in the sequence semi-open $>$ low scrub $>$ solitary trees $>$ tall scrub $>$ open grass and crops $>$ forest (Tab. 1). Randomization tests differentiated between habitat types, and types that did not significantly differ in relative use can be grouped into pools of habitats. This yields three different pools, a preferred habitat pool including semi-open and low scrub habitat types, a tolerated habitat pool containing solitary trees and tall deciduous scrub, and an avoided habitat pool comprising tall bamboo, forest and open country habitat types. Analysis of density and cover categories yielded only one significant difference each. Dense scrub with 5-10 m visibility was preferred over dense scrub with visibility lower than 5 m ($P < 0.05$), but did not differ from other density categories. Areas with 0-20% of ground cover vegetation were preferred ($P < 0.01$) over densely covered areas (81-100% cover), but intermediate cover types were equally

preferred. Average scrub height between 2 and 4 m was significantly preferred over all other scrub heights ($P < 0.01$), which did not differ significantly from each other.

The analysis of point samples between used and unused points of *A. pallidiceps* at the study area scale indicated that bush and herb cover were significantly larger at used points, and grass and tree cover were significantly smaller than at points where *A. pallidiceps* was absent (Tab. 2). Vines and density had significantly higher values at used points. The maximum and average height of the scrub was significantly lower at used than at unused points. Bamboo had slightly larger proportions at used points, but these differences were not significant (Tab. 2). The logistic regression equation chosen when all *A. pallidiceps* sightings were compared to all random points outside territories (unused points) contained seven variables and was selected from among other similar models on the basis of the lowest AIC-value (AIC=546.56, n=822). Variables included were bush, tree and herb cover, density, average height, vines and aspect. The bootstrapping validated model correctly classified 87.2% of points (pseudo- $R^2=0.483$, $AUC_{corrected}=0.873$). Parameter estimates are listed in Table 6.

B. torquatus occupied sites that had significantly higher bush, herb and tree cover than unused sites in the study area (Tab. 3). Maximum and average height of scrub at used points were on average 2-3 m higher than at unused points. Grass covered significantly lower proportions at used than at unused sites, and both vines and density had significantly larger values at used points (Tab. 3). The multivariate analysis of used points versus unused random points yielded a logistic regression model including the five significant ($P < 0.05$) variables aspect, grass cover, vines, density and maximum height (AIC=295.84, n=517; Tab. 6). The bootstrapped model eliminated herb cover as insignificant ($P = 0.343$), and correctly classified 85.4% of all cases (n=517, pseudo- $R^2=0.672$, $AUC_{corrected}=0.930$).

Territory scale

The Pale-headed Brush-Finch did not use all available resources within territories at random. Herb cover and vines were significantly larger at points used by *A. pallidiceps* than on average at available points (Tab. 2). Maximum height of scrub was slightly higher at used than at ran-

dom points within territories. None of the other variables differed significantly between used and available points in territories (Tab. 2). The logistic regression equation included bush, tree and herb cover, vines and density to predict the presence of *A. pallidiceps* in territories (AIC=858.187, n=861), and provided acceptable results in cross-validation tests. The classification of predicted presence values into score bins resulted in a significant positive correlation between predicted presence and bin value for points actually used by *A. pallidiceps* (Spearman $r_s = 0.964$, $P < 0.01$).

B. torquatus was observed at points that had significantly higher proportions of vines, tree and herb cover than on average available in territories (Tab. 4). In turn, bamboo took up significantly lower proportions at used points. Maximum height of the scrub was significantly higher at used than at random points within territories, but average height was not. Inclination was on average higher at available points than at used points. Bush cover, grass cover and density were not significantly different between used and available points within territories (Tab. 4). A logistic regression model with tree, grass, and herb cover, vines and average height as predicting variables was selected among similar models on the basis of the lowest AIC-value (AIC=257.96, n=255). It failed to accurately classify points where *B. torquatus* occurred in territories (5-fold cross-validation, Spearman $r_s < 0.7$, $P > 0.05$).

Nest site selection

A. pallidiceps built nests at sites that had significantly lower tree cover than unused random sites within nest territories (Tab. 5). Nest sites were placed in areas with significantly higher vines and densities than unused random points. Bamboo took up almost 100% at some nest sites, but was entirely absent at others, resulting in average proportions that were slightly larger than average unused sites. Both maximum and average scrub height were slightly lower at nest sites, but these differences were not significant, as were the remaining habitat variables (Tab. 5). The logistic regression model selected using AIC included the variables vines, bamboo, tree and grass cover (AIC=94.550, n=149). The bootstrap validation removed the variables tree and grass cover as they failed to significantly increase the predictive success of the model ($P <$

0.05). The final model included only vines and bamboo and correctly classified 87.9% of all points. (pseudo- $R^2=0.238$, $AUC_{corrected}=0.817$; Tab. 6).

Interspecific comparison

B. torquatus established territories that overlapped with territories of *A. pallidiceps*, and hardly any interspecific aggressions were noted during the study period. On a single occasion, *B. torquatus* unsuccessfully attempted to displace *A. pallidiceps* from a branch. *B. torquatus* occurred in at least 16 of 26 *A. pallidiceps* territories (61.5%), and in one territory the nests of both species were less than 25 m apart. The microhabitat use of both species, as measured by point samples, differed significantly. Habitat points used by *B. torquatus* had significantly higher herb (U-test, $Z = -2.489$, $P < 0.05$), bush ($Z = -14.206$, $P < 0.001$) and tree cover ($Z = -14.047$, $P < 0.001$), and significantly taller maximum ($Z = -13.378$, $P < 0.001$) and average scrub heights ($Z = -11.524$, $P < 0.001$) than those used by *A. pallidiceps*. Grass cover was significantly lower in places where *B. torquatus* was observed ($Z = -13.275$, $P < 0.001$). The proportion of bamboo did not differ significantly between the two species ($Z = -1.046$, $P = 0.296$). *A. pallidiceps* used points with significantly less vines ($Z = -6.480$, $P < 0.001$) and lower density ($Z = -9.273$, $P < 0.001$) than *B. torquatus*, and occurred on average in steeper areas ($Z = -6.335$, $P < 0.001$). The position where the birds were observed differed significantly between the two species ($Z = -7.822$, $P < 0.001$). *B. torquatus* was more often observed on the ground and in lower vegetation strata (127.43 ± 113.50 , $n=142$) than was *A. pallidiceps*, who was on average observed 2 m above the ground (201.33 ± 117.87 , $n=717$). The foraging heights of *A. pallidiceps* decreased significantly with higher proportions of grass cover (linear regression, $B = -0.669$, $r^2 = 0.22$, $P < 0.001$), but this correlation did not persist when the equation was corrected for scrub height. The logistic regression model applied to separate the habitat points used by both species included the variables tree, grass and herb cover, bamboo, density, average scrub height and position ($AIC=256.41$, $n=766$). Bootstrapping confirmed the high accuracy of the model and it accurately classified 92.8% of observations (pseudo- $R^2=0.675$, $AUC_{corrected}=0.953$; Tab. 6).

DISCUSSION

Bias

Various forms of bias are known to affect the results of observational avian studies (Ekman 1981; Machlis et al. 1985; Morrison 1984; Wagner 1981). In this study, the small population of *A. pallidiceps* limited the effective sample size to 26 territories, which is smaller than the 30 required to overcome potential bias from dependent observations or individual abnormalities (Machlis et al. 1985; Morrison 1984). Problems arising from the dependency of consecutive observations were minimized by a minimum time lag of 2 min between consecutive point samples of a single individual.

Owing to the behavior of the brush-finches, changing visibility might introduce bias to the assessment of habitat use. Birds in denser habitats are more difficult to see, therefore open habitat samples might be overrepresented in the data set. This might affect the recorded use of high density habitat by the two brush-finch species studied here, as especially bamboo forms very dense tangles that inhibit observations.

Ideally all individuals should be sampled with an equal effort, thus contributing approximately similar proportions to the data set to minimize bias caused by individual abnormalities (Machlis et al. 1985). Due to the heterogeneity of habitats occupied by different pairs of *A. pallidiceps*, sampling effort was biased towards the more accessible and more vocal pairs to maximize the number of sightings. Deliberately broad categories were used for the mapping at the landscape scale to ensure that habitat types used disproportionately could be identified. The broad categorization might have rendered some variables inconclusive. Due to the lack of detailed maps only relative estimates of habitat use could be determined. A far more intensive methodology would need to be employed to investigate absolute area requirements. This would include the creation of a digital terrain model, and the use of radio-telemetry to determine home ranges more reliably. Such an approach was beyond the resources of this study.

Several methods of analysis for proportional habitat use studies are available, and their performance has been compared on various occasions (Alldredge & Ratti 1986, 1990; McClean et al.

1998). McClean et al. (1998) demonstrated that the Bonferroni-adjusted chi-squared analysis (Neu et al. 1974) provided the most consistent results, however, they noted that the Bonferroni correction might be too conservative to discover small differences. The Bonferroni-tests yielded almost no significant differences between used and available habitat proportions in this study and were therefore rejected in favor of compositional analysis.

One problem arising when a single data set is used to construct statistical models is that the model is overly optimistic, as the parameters are estimated from and tested on the same data (Schröder 2000; Steyerberg et al. 2001). Ideally, a different data set would be obtained to assess the model performance and its predictability (Reineking & Schröder in prep.). This approach was inappropriate in the present study, therefore resampling methods were used to validate models and test for accuracy. (Manel et al. 2001) cautioned the reliance on ROC-curves as a performance measure in predictive modelling. They compared several performance measures and found that ROC-curves, while being independent of prevalence and predefined thresholds, erroneously overestimated true presence when applied to independent test data (Manel et al. 2001). Since in this study modeling was not used for presence predictions outside the study area, the ROC procedure is acceptable (Manel et al. 1999).

Habitat selection of *A. pallidiceps*

The Pale-headed Brush-Finch has been described to occupy dense arid scrub and stands of *Acacia*-trees, often in ravines close to irrigation channels or natural water courses (Carlos & Sornoza 2001; Paynter 1972; Ridgely & Greenfield 2001). This study shows that trees and ravines containing tall woody vegetation are not a preferred habitat type, at least during the breeding season. The most preferred habitat on the landscape scale is a heterogenous semi-open scrubland, where small patches of low scrub are interspersed with grassy clearings or herbfields. Dense continuous scrub adjacent to open areas is similarly preferred, and present in all territories. The nature of the scrub, whether deciduous or bamboo, appeared to be of low relevance, since territories with only one type each were established. Solitary trees like *Acacia* sp. were tolerated in territories, but continuous tall vegetation or woodland was generally avoided by the birds. Some birds occupied areas adjacent to small woodlots, yet those patches were excluded from territories. Territories need to provide a minimum amount of crucial fea-

tures for cover and food supply, and depending on the composition of the landscape, this will lead to the inclusion of irrelevant habitat features (Myserud & Ims 1998). The fact that the smallest territories did neither include open grass nor trees and tall scrub further supports the fact that these resources are of no value to the Pale-headed Brush-Finch.

The avoidance of woodland has been found in other scrub-inhabiting passerines (van den Berg et al. 2001). This has been hypothesized to be either an effect of increased predation risk close to woodlands that serve as perches or breeding sites of avian predators (Lima & Dill 1990; Myserud & Ims 1998; Suhonen 1993; van den Berg et al. 2001), or to stem from a barrier effect of woodland to the dispersal of birds (van den Berg et al. 2001). Both theories are unlikely to influence the distribution of *A. pallidiceps*, when judged from reconstructed natural habitats. Prior to human settlement, the small range of *A. pallidiceps* (Paynter 1972) was probably covered with continuous forest tracts (Blasco et al. 2000; Borchsenius 1997; Bussmann 2001; Dercon et al. 1998). Forest free habitats then likely occurred only after disturbances such as landslides or fires, with scrub habitats dominating successional stages (Bussmann 2001; Paulsch & Czimczik 2001). If this was the natural habitat of *A. pallidiceps* (N. Krabbe *pers. comm.*), it would have naturally always been adjacent to woodland. Therefore other factors, such as prey availability or historic competition, might account for the Pale-headed Brush-Finch's avoidance of forested habitat. The availability and accessibility of food resources has been demonstrated to be the main factor governing habitat use by insectivorous species (Holmes & Robinson 1981; Illera 2001; Keane & Morrison 1999). The possibility that *A. pallidiceps* is excluded from forested habitat by *B. torquatus* is discussed below.

The most preferred scrub vegetation was between 2-4 m high. This was the most common height class in the study area, but was still used proportionately more than available. Furthermore, scrub lower than 2 m and higher than 6 m was consistently avoided, indicating that *A. pallidiceps* specializes on intermediate scrub heights. This supports the above mentioned avoidance of woodland, and provides a further indication for the natural affinity to intermediate successional stages, such as landslide or fire regeneration patches (Bussmann 2001).

At the landscape scale, compositional analysis could not clearly distinguish between density and ground cover categories, suggesting that these factors are more relevant at the microhabitat use scale. The choice of territories appeared to be based on overall vegetation structure and

vegetation height. The logistic regression model yielded similar results, predicting higher probabilities of occurrence with higher bush cover, and lower tree cover and vegetation height. Even though Jones (Jones 2001) stated that use-availability designs are generally more informative, the use vs. non-use comparison in this study yielded more information regarding the habitat selection of *A. pallidiceps* (van den Berg et al. 2001). The model also included density, vines and bamboo as important predictor variables. Bamboo and vines contribute to higher vegetation densities and support the fact that *A. pallidiceps* prefers rather low but dense thickets and tends to avoid open undergrowth under tall woody vegetation.

At the territory level the same variables distinguished between points used by THE PALE-HEADED BRUSH-FINCH and those available. Availability was defined on the basis of territory limits estimated from observations. Territory boundaries did not appear to be stable throughout the breeding season (Oppel et al. in prep.), hence estimates of availability might be skewed, leading to bias in the calculated model (Arthur et al. 1996; McClean et al. 1998). Similar selection processes based on the same factors indicate that the established territory functions only as a coarse filter to eliminate unacceptable macrohabitat. This might offer an explanation for the inability to detect differences between the more subtle habitat variables density and ground cover when using the coarse mapping method. At the landscape scale territories might be selected solely on apparent visual cues such as habitat structure and height, leading to a random inclusion of all categories of other variables, which are then selected for in small-scale habitat use at the territory level. This nested habitat selection that focuses on different habitat features with smaller spatial scales has been demonstrated for a variety of bird species (Bergin 1992; Esely & Bollinger 2001; Luck 2002; Rolstad et al. 2000).

Nest sites formed a small subset of used points in territories. The nests of *A. pallidiceps* have been described to be placed on overhanging branches, vines, and bamboo stalks, and this has been hypothesized to preclude small mammalian predators from reaching the nest (Oppel et al. in prep.). Nest sites are generally selected to minimize detection and predation risk (Martin 1995; Martin & Roper 1988; Martin et al. 2000; van den Berg et al. 2001). Despite being quite variable in density and vegetation height, nest sites could be correctly classified with a logistic regression model using vines and bamboo to distinguish between nest and non-nest sites. The nest site is therefore likely to be selected on the basis of factors immediately affecting nest po-

sitioning. The availability of suitable nest sites, as provided by dense tangles of bamboo or shrubby vines, might therefore be a limiting factor to the distribution of *A. pallidiceps*, which can potentially explain its absence from apparently suitable semi-open low scrub habitat types in the vicinity of the study area, which do not contain vines or bamboo (pers. obs.).

Habitat selection of *B. torquatus*

Results from the multivariate analyses suggest that the Stripe-headed Brush-Finch favors sites with tall vegetation, trees, and dense undergrowth in the study area. Presence probability decreased with increasing grass cover, and increased with taller vegetation, and more vines. This indicates that THE STRIPE-HEADED BRUSH-FINCH avoids open and semi-open habitat types where grass cover is high, probably as a result of its tendency for ground-foraging (Paynter 1978; Remsen & Graves 1995b; Ridgely & Greenfield 2001). The tendency to occur more in southerly or westerly aspects is probably a result of the higher sunshine intensity during the morning hours. This leads to cooler and moister habitats on slopes facing west and south, which is also reflected by lush vegetation in these areas. The Stripe-headed Brush-Finch's preference for moist areas under tall vegetation is consistent with other descriptions of habitat use (Paynter 1978; Remsen & Graves 1995b; Ridgely & Greenfield 2001). Four density categories (1-4) were negatively correlated to the presence probability of *B. torquatus* (Tab. 6). The negative relationship with these categories probably results from THE STRIPE-HEADED BRUSH-FINCH's preference for extremely dense scrub, represented by category 5. When including categorical variables in a logistic regression model, the n-state variable will be divided into n-1 separate variables with binary state information. These n-1 variables assume a zero value (non-use) when the excluded category is used in a certain data set. Thus, the preference of the excluded category will lead to a negative relationship of use with all the other categories included in the model.

Even though several variables were significantly different between used and available points within territories when examined univariately, a multivariate model failed to accurately distinguish used sites from random sites. This indicates that THE STRIPE-HEADED BRUSH-FINCH, unlike THE PALE-HEADED BRUSH-FINCH, chooses territories already very carefully from the available habitat in the study area, so that the area included in territories is almost

entirely suitable. Since no extensive forest tracts were present in the study area, territories inevidently included some marginal habitat, which explains the differences between use and availability of tree and herb cover, vines, bamboo and maximum height. It might, however, be an artefact of the investigation method, which relied on territory boundaries based on expert knowledge. The implicitly assumed territories might have been smaller than actual territories, including the core range, but not the periphery, thus leading to biased estimations of microhabitat selection at the territory scale. Different definitions of availability have been demonstrated to have a large effect on the outcome of resource selection studies (McClellan et al. 1998; Myrnes & Ims 1998).

Interspecific habitat relationships

Interspecific competition and territoriality is a result of similar habitat preferences (Cody 1978; Saether 1983), especially in suboptimal habitats or where vegetation structure is low (Orians & Willson 1964), and has been demonstrated for various bird species (Cody 1978; Elle 2002; Haffer 1967; Orians & Willson 1964; Rice 1978). Similarities in microhabitat use infer fitness costs, hence, natural selection should work towards a divergence of habitat preferences between species (Martin 1996, 1998). Several Andean brush-finches exhibit complementary distribution patterns, which have long been thought to be a result of interspecific competition and competitive exclusion (Fjeldså & Krabbe 1990; Garcia-Moreno & Fjeldså 1999; Renssen & Graves 1995a, b; Terborgh & Weske 1975). The genus *Atlapetes* falls into several species groups (Paynter 1978), and members of different groups are more likely to coexist at a site than are members from the same group (Renssen & Graves 1995a). It is being assumed that, at a locality where two brush-finch species coexist, the two species differ in habitat or microhabitat use (Renssen & Graves 1995a). However, *B. torquatus*, despite belonging to a different species group sensu Paynter (1978), is a vigorous competitor and has been suspected to limit the choice of habitats by *A. pallidiceps* (Agreda et al. 1999). Paynter (1972) attributed the habitat switch of *A. nationi* from forest in the temperate zone to scrubland in the semi-arid subtropical zone to the presence of *B. torquatus* in woodland in the sub-tropical zone. However, the subspecies that Paynter (1972) assumed to belong to *A. nationi* have been given separate species status in the meantime, indicating genetic differences that may reflect on habitat use

At the study area in Yunguilla valley, *A. pallidiceps* and *B. torquatus* occur truly syntopic. Even though *B. torquatus* prefers on average taller and denser vegetation types, the territories of both species overlap widely. This contradicts the theory of interspecific territoriality and competitive exclusion, in which case the territories of both species should not overlap (Cody 1978; Elle 2002; Orians & Willson 1964). Despite overlapping territories, the microhabitat preferences of both species as described above differ markedly. The logistic regression model successfully distinguished between points where *A. pallidiceps* occurred and where *B. torquatus* occurred. Vegetation height and density, and the cover of trees and grass seem to exert a strong influence on the distribution of the two species. *A. pallidiceps* has been described to be more arboreal than other brush-finch species (Paynter 1972), however, in this study it showed a negative relationship with tall vegetation and trees. Areas with trees were more consistently occupied by *B. torquatus*, which conforms with previous descriptions of this species' habitat preferences (Hilty & Brown 1986; Paynter 1978; Ridgely & Greenfield 2001). It has been noted for various subspecies of *A. nazioni*, that it is a forest form in the temperate zone, but occurs in scrub in the semi-arid subtropical zone presumably as a result of *B. torquatus* occupying woodland there (Paynter 1972). It is therefore possible that the two species overlap in shrubby and more open habitat, but that *A. pallidiceps* is excluded from habitat optimal for the dominant *B. torquatus* (Cody 1978; Rice 1978). This might be a result of recent competitive exclusion (Cody 1978; Elle 2002), or historic competition leading to divergent habitat preferences (Martin 1998; Orians & Willson 1964; Pulliam & Enders 1971). Owing to the limited distribution of *A. pallidiceps* the first hypothesis is difficult to test. Circumstantial support may be provided by the separation of foraging strata. Interspecific differences in preferred foraging heights or vegetation strata have been acknowledged as a major factor reducing competition between bird species, and enabling coexistence in certain habitats (James 1976; Murray 1981; Williamson 1971). As has been noted for the co-existing *B. torquatus* and *A. leucopterus* (Paynter 1972), *B. torquatus* and *A. pallidiceps* tend to forage in different strata, with *B. torquatus* being prevalent on or close to the ground (Paynter 1978; Ridgely & Greenfield 2001). Even though ground foraging has also been observed in *A. pallidiceps* (Oppel et al. in prep.; Paynter 1972), mean foraging heights were 2 m above the ground. The position of *A. pallidiceps* decreased with increasing grass cover, a variable negatively correlated with the presence of *B. torquatus* (Tab. 6). While this might indicate the usage of lower foraging

heights otherwise occupied by *B. torquatus*, this difference might be due to the generally lower vegetation height. If grass cover was controlled for scrub heights, no correlation between position of the bird and the combined variable was evident. I therefore conclude that the presence of *B. torquatus* does not limit *A. pallidiceps* to elevated foraging heights, and that the ecological separation demonstrated by the logistic regression model is due to habitat partitioning at a place of coexistence. Microhabitat preferences that reduce competition are adaptive, and occur in species that have been coexisting for evolutionary relevant times (Martin 1998; Orians & Willson 1964). The presence of *B. torquatus* should therefore have no adverse effect on the remaining *A. pallidiceps* population. It has to be cautioned though, that competition might only be evident in times of food scarcity or other stress-inducing circumstances (Pulliam 1985), and that peaceful co-existence is not generally applicable to all states of the environment.

Implications for conservation

If the Pale-headed Brush-Finch is to be preserved in the rapidly changing landscape of southern Ecuador, suitable habitats need to be protected. I have demonstrated that semi-open scrubland with intermediate vegetation height and a large proportion of vines or bamboo appear to be the most suitable habitat at present. Scrub and non-forest vegetation types have been described by (Bussmann 2001) and (Dercon et al. 1998) to belong to the natural vegetation, especially on ridges and after fire damage. Dense *Holcus* sp. grasslands are also known to inhibit the intrusion of shrubs (Kratochwil & Schwabe 2001). However, in the study area succession is considered to lead to a woodier and more forest-like habitat, which has been demonstrated to be avoided by the Pale-headed Brushfinch. The preservation of optimal semi-open habitat would therefore require intensive management to halt succession at an intermediate stage. Grazing did not appear to have a negative effect on the birds, as long as sufficiently dense thickets persist and provide enough cover for nest sites. Given the socio-economic pressures of rural Ecuador, complete exclusion of farming practices would only be feasible at a very high cost. Livestock grazing intensity is known to affect both floristic composition and overall vegetation structure (Ammon & Stacey 1997; Bullock & Pakeman 1997), and thus may influence habitat selection by birds (Rotenberry 1985). Therefore it would be desirable to come to an agreement with local farmers who hold potential brush-finch habitat, to ensure that (1) scrubland is not con-

verted to arable fields by the burning of vegetation, and (2) grazing pressure is maintained at an intermediate level to preserve dense thickets. The latter could be achieved by a rotational system, where parts of a brush-finch reserve are grazed alternately within or between years.

The invasion of bracken fern (*Pteridium aquilinum*) is a problem to many farmers, since it renders grassland ineffective for grazing, and also prevents natural succession (Paulsch et al. 2001). Fallow areas, that have been abandoned following the invasion of ferns, should be afforested with scrub species to convert them to suitable habitat.

The presumed absence of birds from small isolated patches of suitable habitat needs to be clarified (Opell et al. in prep.). It would indicate that a conservation plan for this species should include the maintenance of large patches with appropriate landscape and microhabitat features, rather than several small reserves (Gates & Donald 2000; Simberloff 1994). Still, the natural habitat of the Pale-headed Brush-Finch is uncertain. I have mentioned that successional stages after natural landslides or fires could probably have provided sufficient forest free habitat (Bussmann 2001). However, these patches would have been spaced apart and would have required considerable dispersal abilities. Dispersal abilities might have been well developed in the Pale-headed Brush-finch occupying a largely forested landscape, but it has been demonstrated for a variety of species that dispersal ability might drop sharply with the fragmentation and loss of natural habitat, as this increases the mortality on transition through matrix habitat (Fahrig 2001; Gibbs 1998; Lang et al. 2002). The highly fragmented and largely open landscape of the Pale-headed Brush-Finch's assumed range in the upper Rio Jubones drainage (Paynter 1972) is therefore likely to exert a strong limitation on dispersal and subsequent recolonization of suitable habitat patches. The current dispersal abilities of the Pale-headed Brush-Finch need to be investigated further, and inhibitors need to be identified, to develop a management plan that focuses at a larger scale than a single reserve. The population viability and extinction probability also needs to be assessed, in order to find reserves that maximize chances for success (Araújo et al. 2002). A network of reserves would be desirable to provide refuges for sporadically occurring climatic events (Winker et al. 1997).

Water courses have been mentioned to be an important requisite for Pale-headed Brush-Finches in the semi-arid landscape (Agreda et al. 1999; Carlos & Sornoza 2001; Paynter 1972; Ridgely & Greenfield 2001). The present study was carried out during the breeding season, shortly after the wet season, when ephemeral water is still common in small gullies and depres-

sions. These water patches dry up during the dry season, and it has to be determined whether the distribution of the birds changes throughout the year, and whether water plays an important role for the general habitat suitability of the Pale-headed Brush-Finch.

REFERENCES

- Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* **74**:1313-1323.
- Agreda, A., N. Krabbe, and O. Rodriguez. 1999. Pale-headed Brushfinch *Atlapetes pallidiceps* is not extinct. *Cotinga* **11**:50-54.
- Alldredge, J. R., and J. T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. *Journal of Wildlife Management* **50**:157-165.
- Alldredge, J. R., and J. T. Ratti. 1990. Further comparison of some statistical techniques for analysis of resource selection. *Journal of Wildlife Management* **56**:1-9.
- Ammon, E. M., and P. B. Stacey. 1997. Avian nest success in relation to past grazing regimes in a montane riparian system. *Condor* **99**:7-13.
- Araujo, M. B., P. H. Williams, and R. J. Fuller. 2002. Dynamics of extinction and the selection of nature reserves. *Proceedings of the Royal Society* **269**:1971-1980.
- Araújo, M. B., P. H. Williams, and R. J. Fuller. 2002. Dynamics of extinction and the selection of nature reserves. *Proceedings of the Royal Society* **269**:1971-1980.
- Arthur, S. M., B. F. J. Manly, L. L. McDonald, and G. W. Garner. 1996. Assessing habitat selection when availability changes. *Ecology* **77**:215-227.
- Austin, G. E., C. J. Thomas, D. C. Houston, and D. B. A. Thompson. 1996. Predicting the spatial distribution of buzzard *Buteo buteo* nesting areas using a Geographical Information System and remote sensing. *Journal of Applied Ecology* **33**:1541-1550.
- Beck, J. R., and E. K. Shultz. 1986. The use of relative operating characteristic (ROC) curves in test performance evaluation. **110**:13-20.
- Bergin, T. M. 1992. Habitat selection by the western Kingbird in western Nebraska: a hierarchical analysis. *Condor* **94**.
- BirdLifeInternational 2000. Threatened birds of the world. Lynx Edition and BirdLife International, Barcelona and Cambridge.
- Blasco, F., T. C. Whitmore, and C. Gers. 2000. A framework for the worldwide comparison of tropical woody vegetation types. *Biological Conservation* **95**:175-189.
- Borchsenius, F. 1997. Patterns of plant species endemism in Ecuador. *Biodiversity and Conservation* **6**:379-399.
- Bossuyt, B., G. Dercon, B. D. Bièvre, F. Cisneros, and J. Deckers. 1997. Agro-ecological zoning of the Austro Ecuatoriano. *The Land* **1**:159-170.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* **157**:281-300.
- Buckland, S. T., K. P. Burnham, and N. H. Augustin. 1997. Model selection: an integral part of inference. *Biometrics* **53**:603-618.

- Bullock, J. M., and R. J. Pakeman. 1997. Grazing of lowland heatherland: management methods and their effects on heatherland vegetation. *Biological Conservation* **79**:1-13.
- Burnham, K. P., and D. R. Anderson. 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. Pages 16-30 in D. R. McCullough, and R. H. Barrett, editors. *Wildlife 2001: Populations*, based on an international conference on population dynamics and management of vertebrates (exclusive of primates and fish) held at Oakland, California, USA, July 29-31 1991. Elsevier Applied Science, London, New York.
- Bussmann, R. W. 2001. The montane forests of Reserva Biologica San Francisco (Zamora-Chinchipe, Ecuador): Vegetation zonation and natural regeneration. *Die Erde* **132**:9-25.
- Carlos, B., and F. Sornoza. 2001. Report on new population of *Atlapetes pallidiceps* discovered. Pages 1-3. Fundacion Jocotoco, Quito.
- Chatfield, C. 1995. Model Uncertainty, Data mining and Statistical Inference. *Journal of the Royal Statistical Society / A* **158**:419-466.
- Cody, M. L. 1978. Habitat selection and interspecific territoriality among the Sylviid warblers of England and Sweden. *Ecological Monographs* **48**:351-396.
- Collar, N. J., L. P. Gonzaga, N. Krabbe, A. M. Nieto, L. G. Naranjo, T. A. Parker, and D. C. Wege 1992. *Threatened birds of the Americas*. International Council for Bird Preservation, Cambridge.
- Dercon, G., B. Bossuyt, B. D. Bièvre, F. Cisneros, and J. Deckers 1998. *Zonificación agroecológica del Austro Ecuatoriano*. Promas, Universidad de Cuenca, Cuenca, Ecuador.
- Ekman, J. 1981. Problems of unequal observability. *Studies in Avian Biology* **6**:230-234.
- Elle, O. 2002. Mikrohabitatwahl und Dispersion als Hinweise auf interspezifische Konkurrenz von Mönchsgrasmücke *Sylvia atricapilla* und Gartengrasmücke *S. borin* in einem Wald-Wiesen-Ökoton. *Vogelwelt* **123**:9-16.
- Esely, J. D., and K. D. Bollinger. 2001. Habitat selection and reproductive success of loggerhead shrikes in northwest Missouri: A hierarchical approach. *Wilson Bulletin* **113**:290-296.
- Fahrig, L. 2001. How much habitat is enough? *Biological Conservation* **100**:65-74.
- Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* **24**:38-49.
- Fjeldså, J., and N. Krabbe 1990. *Birds of the high Andes*. Zoological Museum, University of Copenhagen, Copenhagen.
- Garcia-Moreno, J., and J. Fjeldså. 1999. Re-evaluation of species limits in the genus *Atlapetes* based on mtDNA sequence data. *Ibis* **141**:199-207.
- Gates, S., and P. F. Donald. 2000. Local extinction of British farmland birds and the prediction of further loss. *Journal of Applied Ecology* **37**:806-820.
- Gibbs, J. P. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. *Landscape Ecology* **13**:263-268.
- Gottschalk, T. 1995. Habitatanalyse von Singvogelarten unter Verwendung eines Geographischen Informationssystems (GIS). *Vogelwelt* **116**:273-284.
- Graham, C. 2001. Habitat selection and activity budgets of Keel-billed Toucans at the landscape level. *Condor* **103**:776-784.
- Haffer, J. 1967. unknown. *Hornero* **10**:438-440.

- Henley, J. A., and B. J. McNeil. 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology* **143**:29-36.
- Hildén, O. 1965. Habitat selection in birds - a review. *Annales Zoologici Fennici* **2**:53-75.
- Hilty, S. L., and W. L. Brown 1986. A guide to the birds of Colombia. Princeton University Press, Princeton.
- Holmes, R. T., and S. K. Robinson. 1981. Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. *Oecologia* **48**:31-35.
- Hosmer, D. W., and S. Lemeshow 2000. Applied logistic regression. John Wiley, New York.
- Illera, J. C. 2001. Habitat selection by the Canary Islands stonechat (*Saxicola dacotiae*) (Meade-Waldo, 1889) in Fuerteventura Island: a two-tier approach with implications for management. *Biological Conservation* **97**:339-345.
- James, R. D. 1976. Foraging behavior and habitat selection of three species of vireos in Southern Ontario. *Wilson Bulletin* **88**:62-75.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**:65-71.
- Jones, J. 2001. Habitat selection in avian ecology: a critical review. *Auk* **118**:557-562.
- Keane, J. J., and M. L. Morrison. 1999. Temporal variation in resource use by Black-throated Gray Warblers. *Condor* **101**:67-75.
- Kratochwil, A., and A. Schwabe 2001. *Ökologie der Lebensgemeinschaften - Biozönologie*. Eugen Ulmer, Stuttgart.
- Lang, J. D., L. A. Powell, D. G. Krementz, and M. J. Conroy. 2002. Wood Thrush movements and habitat use: effects of forest management for Red-cockaded Woodpeckers. *Auk* **119**:109-124.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**:619-640.
- Luck, G. W. 2002. The habitat requirements of the rufous treecreeper (*Climacteris rufa*). 1. Preferential habitat use demonstrated at multiple spatial scales. *Biological Conservation* **105**:383-394.
- Machlis, L., P. W. D. Dodd, and J. C. Fentress. 1985. The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. *Zeitschrift für Tierpsychologie* **68**:201-214.
- Manel, S., J. M. Dias, S. T. Buckton, and S. J. Ormerod. 1999. Alternative methods for predicting species distribution: an illustration with Himalayan river birds. *Journal of Applied Ecology* **36**:734-747.
- Manel, S., H. C. Williams, and S. J. Ormerod. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* **38**:921-931.
- Manly, B. F. J. 1997. Randomization, bootstrap and Monte Carlo methods in biology. Chapman & Hall, London.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* **65**:101-127.
- Martin, T. E. 1996. Fitness costs of resource overlap among coexisting bird species. *Nature* **380**:338-340.
- Martin, T. E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology* **79**:656-670.
- Martin, T. E., and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* **64**:507-519.

- Martin, T. E., and J. J. Roper. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. *Condor* **90**:51-57.
- Martin, T. E., J. Scott, and C. Menge. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society* **267**:2287-2293.
- McClellan, S. A., M. A. Rumble, R. M. King, and W. L. Baker. 1998. Evaluation of resource selection methods with different definitions of availability. *Journal of Wildlife Management* **62**:793-801.
- Morrison, M. L. 1984. Influence of sample size and sampling design on analysis of avian foraging behavior. *Condor* **86**:146-150.
- Murray, B. G. 1981. The ecological consequences of interspecific territorial behavior in birds. *Ecology* **52**:414-423.
- Mysterud, A., and R. A. Ims. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology* **79**:1435-1441.
- Naugle, D. E., K. F. Higgins, S. M. Nusser, and W. C. Johnson. 1999. Scale-dependent habitat use in three species of prairie wetland birds. *Landscape Ecology* **14**:267-276.
- Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management* **38**:541-545.
- Oppel, S., H. M. Schäfer, and V. Schmidt. in prep. First description of the nest, eggs and breeding behavior of the Pale-headed Brush-Finch in Ecuador. *Wilson Bulletin*.
- Orians, G. H., and M. F. Willson. 1964. Interspecific territories of birds. *Ecology* **45**:736-745.
- Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. *American Naturalist* **137**:S29-S49.
- Paulsch, A., and C. I. Czimczik. 2001. Classification of tropical montane shrub vegetation - a structural approach. *Die Erde* **132**:27-41.
- Paulsch, A., R. Schneider, and K. Hartig. 2001. Land-use induced vegetation structure in a montane region of Southern Ecuador. *Die Erde* **132**:93-102.
- Paynter, R. A. 1972. Biology and evolution of the *Atlapetes schistaceus* species-group. *Bulletin Museum of Comparative Zoology* **143**:297-320.
- Paynter, R. A. 1978. Biology and evolution of the avian genus *Atlapetes*. *Bulletin Museum of Comparative Zoology* **148**:323-369.
- Pulliam, H. R. 1985. Foraging efficiency, resource partitioning, and the coexistence of sparrow species. *Ecology* **66**:1829-1836.
- Pulliam, H. R., and F. Enders. 1971. The feeding ecology of five sympatric finch species. *Ecology* **52**:557-566.
- Ratcliffe, C. S., and T. M. Crowe. 2001. Habitat utilisation and home range size of helmeted guineafowl (*Numida meleagris*) in the Midlands of KwaZulu-Natal province, South Africa. *Biological Conservation* **98**:333-345.
- Reineking, B., and B. Schröder. in prep. Computer-intensive methods in the analysis of species-habitat relationships.
- Remsen, J. V., and W. S. Graves. 1995a. Distribution patterns and zoogeography of *Atlapetes* brush-finches (Emberizinae) of the Andes. *Auk* **112**:210-224.
- Remsen, J. V., and W. S. Graves. 1995b. Distribution patterns of *Buarremon* brush-finches (Emberizinae) and interspecific competition in Andean birds. *Auk* **112**:225-236.
- Rice, J. 1978. Ecological relationships of two interspecifically territorial Vireos. *Ecology* **59**:526-538.

- Ridgely, R. S., and P. J. Greenfield 2001. The Birds of Ecuador - Field Guide. Cornell University Press, New York.
- Rolstad, J., B. Løken, and E. Rolstad. 2000. Habitat selection as a hierarchical spatial process: the green woodpecker at the northern edge of its distribution range. *Oecologia* **124**:116-129.
- Rotenberry, J. T. 1985. The role of habitat in avian community composition: physiognomy or floristics? *Oecologia* **67**:213-217.
- Saether, B.-E. 1983. Habitat selection, foraging niches and horizontal spacing of Willow Warbler *Phylloscopus trochilus* and Chiffchaff *P. collybita* in an area of sympatry. *Ibis* **125**:24-32.
- Sandkühler, K., and B. Schröder. 1999. GIS-unterstützte Habitatstrukturanalyse wiesenbrütender Kleinvögel im Drömling (O-Niedersachsen). *NNA-Berichte* **3/99**:41-50.
- Schooley, R. L. 1994. Annual variation in habitat selection: patterns concealed by pooled data. *Journal of Wildlife Management* **58**:367-374.
- Schröder, B. 2000. Habitatmodelle für ein modernes Naturschutzmanagement.
- Schultz, J. 1988. Die Ökozonen der Erde. Eugen Ulmer, Stuttgart.
- Simberloff, D. 1994. Die Konzeption von Naturreservaten. Pages 274-291 in M. B. Usher, and W. Erz, editors. Erfassen und Bewerten im Naturschutz. Quelle und Meyer, Heidelberg.
- Sokal, R. R., and F. J. Rohlf 1981. Biometry. W. H. Freeman, New York.
- Steyerberg, E. W., F. E. H. Jr, G. J. J. M. Borsboom, M. J. C. Eijkemans, Y. Vergouwe, and J. D. F. Habbema. 2001. Internal validation of predictive models: efficiency of some procedures for logistic regression analysis. *Journal of Clinical Epidemiology* **54**:774-781.
- Suhonen, J. 1993. Predation risk influences the use of foraging sites by tits. *Ecology* **74**:1197-1203.
- Terborgh, J., and J. S. Weske. 1975. The role of competition in the distribution of Andean birds. *Ecology* **56**:562-576.
- van den Berg, L. J. L., J. M. Bullock, R. T. Clarke, R. H. W. Langston, and R. J. Rose. 2001. Territory selection by the Dartford warbler (*Sylvia undata*) in Dorset, England: the role of vegetation type, habitat fragmentation and population size. *Biological Conservation* **101**:217-228.
- Verbyla, D. L., and J. A. Litvaitis. 1989. Resampling methods for evaluating classification accuracy of wildlife habitat models. *Environmental Management* **13**:783-787.
- Wagner, J. L. 1981. Visibility and bias in avian foraging data. *Condor* **83**:263-264.
- Wiens, J. A., J. T. Rotenberry, and B. V. Horne. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. *Oikos* **48**:132-147.
- Williamson, P. 1971. Feeding ecology of the Red-eyed Vireo (*Vireo olivaceus*) and assorted foliage-gleaning birds. *Ecological Monographs* **41**:129-152.
- Winker, K., P. Escalante, J. H. Rappole, M. A. Ramos, R. J. Oehlenschläger, and D. W. Warner. 1997. Periodic migration and lowland forest refugia in a "sedentary" Neotropical bird, Wetmore's Bush Tanager. *Conservation Biology* **11**:692-697.
- Zweig, M. H., and G. Campbell. 1993. Receiver-operating characteristic (ROC) plots: a fundamental evaluation tool in clinical medicine. *Clinical Chemistry* **39**:561-577.

CHAPTER THREE

COWBIRD PARASITISM OF THE PALE-HEADED BRUSH-FINCH, *ATLAPETES PALLIDICEPS*: IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

ABSTRACT – The Pale-headed Brush-Finch, *Atlapetes pallidiceps*, is an endemic species that is threatened with extinction due to the loss of habitat. A breeding success survey in 2002 revealed a generally low reproductive output that was likely being caused by parasitism of Shiny Cowbirds, *Molothrus bonariensis*. Parasitism rates exceeded 50 % in a reserve and were 38.5 % for the entire population consisting of c. 60 Individuals. While the breeding success was significantly lower in an un-grazed reserve than in a grazed control plot, this was not attributable to vegetation parameters describing the habitat use and territory composition of the Pale-headed Brush-Finch. Cowbird parasitism rates therefore seem to be influenced largely by factors operating at the landscape level, and it is suggested that lower species diversity and bird abundance render the grazed site less attractive to cowbirds.

Due to the low population size of the Pale-headed Brush-Finch, current parasitism rates are of great conservation concern. Management options described from intensive cowbird control programs in North America are reviewed and evaluated for their applicability to the Pale-headed Brush-Finch. To combine the possibility of further data collection with a commencement of immediate conservation action, nest monitoring and cowbird egg removal is suggested for the following breeding season. Intensive trapping and the resumption of extensive grazing in the reserve needs to be considered for the intermediate future.

1. 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 Rio Jubones drainage in southern Ecuador, with an estimated population of 60-80 Individuals (Collar et al. 1992; Agreda et al. 1999; BirdLife International 2000; Krabbe in prep.). While habitat loss

from human landscape modification appears to be the main factor responsible for the limited distribution of the Pale-headed Brush-Finch, the absence of birds from suitable habitat within its former range indicate that other factors may contribute to its decline (Krabbe in prep.). The detrimental impact of brood parasitism by cowbirds has been identified to have caused declines in sensitive species of limited geographic distribution (Brittingham & Temple 1983; DeCapita 2000; Rothstein & Cook 2000).

Many cowbirds (Aves: Icteridae) are obligate brood parasites of North and South America (Johnsgard 1997; Payne 1997). They are largely associated with open forests and non-forest habitats (Coker & Capen 1995; Burhans 1997; Johnsgard 1997; Strausberger 2001) and have therefore benefited to a great extent from anthropogenic landscape modification (Rothstein & Robinson 1994; Donovan et al. 2000; Petit & Petit 2000; Ward & Smith 2000b). The range of many cowbirds has expanded following the conversion of forest into fragmented and open habitat (Brittingham & Temple 1983; Peterjohn et al. 2000; Rothstein & Robinson 2000; Smith & Rothstein 2000).

Cowbirds adversely affect the breeding success of their hosts through predation (McLaren & Sealy 2000), egg punctures (Massoni & Reboreda 2002), ejection of eggs and nestlings (Dearborn 1996; Wood & Bollinger 1997; Granfors et al. 2001), and competition between nestlings (Dearborn 1998; Lichtenstein & 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 highest predation rates (Cruz et al. 1995), and the spread of cowbirds has often lead to the decline or even local extinction of heavily parasitized host populations (Rothstein & Cook 2000).

The most widespread brood parasite of South America, the Shiny Cowbird, *Molothrus bonariensis* (Payne 1997), has considerably expanded its range in the last decades (Fulton 1990; Baltz 1995; Cruz et al. 1995; Kluza 1998; Marin 2000). It is a generalist brood parasite that has been recorded to parasitize 246 different species (Fraga 2002). The Shiny Cowbird is present in large numbers in the Rio Jubones drainage of southern Ecuador (N. Krabbe & F. Sornoza, *pers. comm.*), and has been observed to parasitize the Pale-headed Brush-Finch. Cowbird parasitism is considered to have detrimental effects on the localized population of the Pale-headed Brush-Finch (Krabbe in prep.).

The Pale-headed Brush-Finch was re-discovered in 1998, and its breeding success and the impact of cowbird parasitism have not been quantified so far. From March through July 2002 I surveyed the entire population and tried to determine breeding success and factors affecting the reproductive output of the species. Specifically I examined whether (1) the Shiny Cowbird parasitizes a significant part of the population, and (2) whether habitat differences can account for varying breeding success between pairs. Since the population is currently spread over two hills with different land use patterns, I was further able to analyze whether current management schemes are beneficial for the Pale-headed Brush-Finch, and whether new management measures are required to secure the population.

2. METHODS

2.1 Study area

The study area is located in Yunguilla Valley, approximately 50 km southwest of Cuenca in the upper Rio Jubones drainage, Province 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 Rio Jubones valley and the humid upper reaches of the Andean west slope (Dercon et al. 1998). Mean annual precipitation, mean temperatures, and growing season differ strongly on a local scale depending on elevation and rain shadow. The study area has an estimated growing season of 5-7 months, and 3-5 humid months with an annual rainfall of 700 - 1000 mm (Bossuyt et al. 1997). The region is intensively farmed, with corn crops and cattle pastures being the most dominant forms of land use (Bossuyt et al. 1997; 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 1650 – 2100 m in elevation. One hill has been declared a reserve and is largely un-grazed, whereas a subsequently discovered population on the neighboring hill inhabits an area that is still grazed by cattle (Carlos & Sornoza 2001). Both hills feature semi-open habitats with dense arid scrub consisting mostly of composite and verbanaceous species, interspersed with grassland of old or recent pastures. Small stands of *Acacia* and lauraceous trees are found in more humid parts, and fragments of semi-humid forest persist on western and southern slopes. Monocultural stands of dwarf bamboo (*Chusquea* spec.) form large patches of habitat in small depressions, ravines, and on the western slopes.

2.2 Breeding success survey

Birds were monitored from first daylight to early afternoon every day from late March to early July 2002. Nests were searched using standard techniques (Martin & Geupel 1993), and the outcome was monitored by regular visits (see Chapter 1 for details). If nests were found to be empty, the nest contents and surroundings were checked carefully 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 eight days of the last egg stage visit, and (3) empty nests were found and both adults could be observed for 60 consecutive minutes without feeding fledglings. Breeding was defined successful if a pair was confirmed to lead at least one dependent brush-finch fledgling. 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, I defined every pair successful that raised at least one brush-finch fledgling throughout the season. All pairs that were not recorded to lead brush-finch offspring were labeled unsuccessful. For habitat analysis, territories that were held by solitary males were included in the unsuccessful category, since failure to attract a partner might indicate poor quality of the male or its chosen territory.

2.3 Habitat measurements

Current land use provided a useful division of the population into those pairs inhabiting the un-grazed reserve, and those with territories on the grazed hill. I used the data derived from habitat mapping (see Chapter 2.2 for detailed description) and point sampling (Chapter 2.3) for analysis of differences between pairs. Land use scheme (grazed or un-grazed) was included as new explanatory variable in each data set.

2.4. Statistical analysis

Land use patterns and habitat characteristics often exert strong effects on the reproductive success of a bird species (Ammon & Stacey 1997; Bradbury et al. 2000; Gates & Donald 2000; Esely & Bollinger 2001; Larison et al. 2001; Rodewald & Yahner 2001). I examined

whether habitat variables recorded with the mapping and point sampling method (Chapter 2.2 and 2.3) were able to differentiate between successful and unsuccessful pairs in the study area.

All territory habitat data and all point observation data were classified as grazed or un-grazed, and successful or unsuccessful, respectively. I used the definitions outlined above, and assigned each pair only one category of each of the variables.

After univariate comparisons using Mann-Whitney-*U*-test, the logistic regression approach as described in Chapter 2.4 was applied, with nesting success as dependent variable. First I tested whether territories differed in their available structural composition by using the mapped habitat variables. To account for size differences of habitat feature polygons, and to obtain linearly independent data, I multiplied the value of each variable with the area of its respective polygon. Then the point observations were used to analyze whether successful and unsuccessful pairs exhibit different micro-habitat use patterns. The model selection and validation procedure was analogous to Chapter 2.4.

The breeding success between pairs in the grazed and un-grazed parts was compared using χ^2 - analysis.

3. RESULTS

During the 2002 breeding survey, a total of 26 territories of the Pale-headed Brush-Finch were found, of which three were held by solitary males. I found 18 nests (see Chapter 1), and recorded another seven broods by the observation of adults leading dependent fledglings within their territories. Of the 25 recorded breeding attempts, 10 were successful and in total 17 fledglings of the Pale-headed Brush-Finch were raised in the study area. This corresponds to an average reproductive output of 0.74 young per breeding pair (or 0.65 per territory).

At least 10 broods were parasitized by the Shiny Cowbird, leading to a total of eight cowbird fledglings being raised by the Pale-headed Brushfinch. Two nests were deserted after being parasitized, and six nests were predated by unknown predators. In four of these it could not be assessed whether they had been parasitized. The minimum overall parasitism rate is 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 9 pairs in the grazed area was significantly higher than of the 14 pairs in the un-grazed reserve ($\chi^2 = 9.04$, d.f. = 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 (Tab. 3.1). Parasitism by the Shiny Cowbird was more prevalent in the reserve, with at least 55 % of all breeding attempts being parasitized.

Table 3.1 Breeding success of the Pale-headed Brush-Finch during the 2002 season in Yunguilla Valley, Ecuador, compared between the un-grazed reserve and an approximately equally large grazed area. Note that predation and parasitism rates are minimum figures only.

	Yunguilla reserve ungrazed	Pasture grazed
Number of pairs	14	9
breeding attempts recorded	18	7
pairs without recorded broods	3	2
Number of nests found	16	2
predated or deserted nests	9	0
parasitized nests	8	1
successful broods	4	6
parasitized broods	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	53 %	14 %
predation rate	44 %	0

Comparing the structural composition between successful and unsuccessful territories of the Pale-headed Brush-Finch by area corrected habitat feature polygons, only intermediate density was significantly higher in successful pairs ($Z = -2.29$, $P = 0.021$). No other difference in habitat composition was apparent between successful and unsuccessful pairs. All backward stepwise logistic regression models retained the variables grazing scheme and grass height as significant predictor variables (Tab 3.2). The best model (AIC = 383.35) was able to accurately classify 74.2 % of observations at a cut-off point of 0.5 (AUC = 0.749, Nagelkerke- $R^2 = 0.205$, $n = 341$).

Table 3.2 Logistic regression coefficients of habitat variables differentiating between successful and unsuccessful pairs of the Pale-headed Brush-Finch in Yunguilla Valley, Ecuador. AUC_{corrected} denotes the area under the receiver-operating characteristic curve after internal validation with bootstrapping. R^2 after Nagelkerke (1984).

Variables	structural composition of territories (n = 341)		micro-habitat use (n = 746)	
	coefficient	<i>P</i>	coefficient	<i>P</i>
grazing scheme	1.913	< 0.001	1.359	< 0.001
grass height (cm)	5.41×10^{-5}	0.020		
bamboo (%)			0.008	0.008
vines (1-5)			0.162	0.043
maximum height (cm)			-0.001	0.029
aspect (sin transformed)			0.771	< 0.001
AUC _{corrected}	0.749		0.676	
Nagelkerke R^2	0.205		0.132	

Univariate analysis of micro-habitat use as described by point observations indicated that successful pairs used points with lower grass cover, and higher bush cover (Tab. 3.3). The best logistic regression model retained grazing scheme, aspect, bamboo, vines and maximum

vegetation height as predictor variables (AIC = 982.792, $n = 742$, Tab. 3.2). It had only limited ability to correctly classify breeding success (AUC = 0.676, Nagelkerke- $R^2 = 0.132$).

Table 3.3 Micro-habitat use of Pale-headed Brush-Finch pairs successfully raising offspring vs. pairs that failed to raise offspring in the 2002 breeding season in Yunguilla Valley, Ecuador. Results are given as mean \pm s.d., Z and P -values from Mann-Whitney U -test.

	successful pairs (n=284)	unsuccessful pairs (n=462)	Z	P
bush cover (%)	68.08 \pm 25.60	64.56 \pm 25.43	-1.97	0.048
tree cover (%)	4.21 \pm 11.27	4.68 \pm 11.15	-1.38	0.250
grass cover (%)	26.90 \pm 27.02	32.52 \pm 26.82	-1.97	0.002
herb cover (%)	19.33 \pm 16.08	18.60 \pm 16.56	-1.38	0.331
bamboo (%)	23.45 \pm 30.23	21.56 \pm 31.35	-3.17	0.253
vines (1-5)	2.18 \pm 1.076	2.09 \pm 1.13	-0.97	0.157
density (1-5)	3.08 \pm 0.99	3.12 \pm 1.08	-1.14	0.466
maximum height (cm)	455.99 \pm 171.77	464.89 \pm 177.28	-1.41	0.310
average height (cm)	277.78 \pm 96.25	273.72 \pm 91.95	-0.73	0.995

4. DISCUSSION

The results demonstrate that the Pale-headed Brush-Finch is exposed to heavy cowbird parasitism within the reserve (Tab. 3.1). Parasitism rates revealed in this study are minimum figures only, since nests were not monitored on a regular basis and unsuccessful parasitism attempts might have gone unnoticed. Table 3.1 also suggests that predation rates were significantly higher in the reserve than in the grazed area, and approximately as high as parasitism rates. The detection of nest predation requires more intensive monitoring, and due to the unequal observation effort between grazed and un-grazed sites I consider the bias too large to derive valid assumptions of nest predation rates. They will therefore not be analyzed

here. Instead, I assume that parasitism by Shiny Cowbirds is one of the main factors contributing to the differences in breeding success. It has to be cautioned though, that cowbird parasitism might have only caused 50 % of failures.

4.1 Factors influencing breeding success

Nest concealment and structural diversity of under-story vegetation are frequently found to affect cowbird parasitism rates of songbirds (Burhans 1997; Larison et al. 1998; Staab & Morrison 1999; Tewksbury et al. 1999; Uyehara & Whitfield 2000). Both the univariate comparisons and the multivariate logistic regression approach indicated that structural differences between successful and unsuccessful territories of the Pale-headed Brush-Finch are relatively small. The logistic regression model analyzing territory structure included only grazing and grass height as variables differentiating between successful and unsuccessful pairs. This indicates that land use has an overriding effect on nesting success that is not explained by vegetation structure within territories. This is further corroborated by the analysis of habitat use, which also suggests that grazing is strongly positively correlated with breeding success (Tab. 3.3). Successful pairs used more bamboo and more vines. These two components have been shown to be crucial to nest site selection (see Chapter 2), and this has been hypothesized to prevent predation by small mammals (see Chapter 1). The positive correlation between vines and bamboo and breeding success might therefore be more related to reduced predation than cowbird parasitism.

Despite supportive evidence that vegetation structure around the nest site can influence parasitism rates (Brittingham & Temple 1996; Larison et al. 1998; Staab & Morrison 1999; Strausberger 2001), there are studies that failed to detect differences of vegetation between parasitized and un-parasitized nest sites (Anderson & Storer 1976; Freeman et al. 1990; Curson 1996). Other factors, like the proximity of perches (Freeman et al. 1990; Clotfelter 1998; Hauber & Russo 2000), and individual host behavior (Curson 1996; Clotfelter 1998; Hauber & Russo 2000) have been assumed to influence parasitism in these cases. No data are available for perch site distribution in Pale-headed Brush-Finch territories, but anecdotal data indicate that parasitized males were singing more frequently and closer to nest sites than unparasitized males (pers. obs.). Higher singing activity might have facilitated nest-finding of female cowbirds (Clotfelter 1998; Hauber & Russo 2000).

Differences of micro-habitat use and vegetation structure within territories are unlikely to affect cowbird parasitism of the Pale-headed Brush-Finch, but individual behavior might deserve quantitative exploration.

If vegetation structure within territories is not sufficiently different to explain elevated parasitism levels, factors that operate at the landscape scale may govern the distribution of cowbirds (Tewksbury et al. 1999; Young & Hutto 1999). Burhans (1997) suggested that cowbird habitat preferences or host choice at a landscape scale might contribute to differences in parasitism. The only landscape attribute that distinguishes the two Pale-headed Brush-Finch sub-populations is the current grazing pattern. The immediate proximity of both sites renders it unlikely that the distance to feeding areas can account for differences in cowbird abundance (Donovan et al. 2000).

The presence of livestock is generally believed to increase parasitism rates of songbirds (Goguen & Mathews 1999). In contrast, this study suggests that grazing is negatively correlated with cowbird parasitism of the Pale-headed Brush-Finch, and pairs in the grazed area are significantly more successful than pairs in the un-grazed reserve (Tab. 3.1). Livestock often provide food resources for cowbirds (Goguen & Mathews 1999), but they also alter the habitat to the detriment of many cowbird host species (Dufty 2000). Grazed areas are often poorer in bird species diversity and abundance (Taylor 1986; Ammon & Stacey 1997; Dobkin et al. 1998; Goguen & Mathews 1998), and it has been demonstrated that cowbirds might choose their breeding areas with respect to a high diversity and abundance of potential hosts (Barber & Martin 1997; Robinson et al. 1999; Tewksbury et al. 1999; Young & Hutto 1999). The reserve was excluded from grazing in 1999, and exhibits a succession towards a structurally more diverse vegetation. The recovery of a diverse avifauna three to four years after livestock removal has been demonstrated in other places (Dobkin et al. 1998). A regenerating avifauna within the reserve might have therefore attracted larger numbers of cowbirds. Anecdotal evidence suggests that both cowbird and other songbird abundance were higher in the reserve than on the grazed slope, but a more quantitative approach needs to be applied to support this hypothesis.

Another feature that has been assumed to influence cowbird distribution and abundance at the landscape scale is topography (Tewksbury et al. 1999). In a study in Montana, USA, Tewksbury et al. (1999) found that Brown-headed Cowbirds (*Molothrus ater*) consistently avoided steep-sided canyons, and this effect was still apparent when controlled for vegetation and host density. While a convincing explanation is still lacking, this effect might have also

affected parasitism rates in the Yunguilla Valley. All parasitized nests, including the only one in the grazed area, were on open convex east-facing slopes, while pairs on the steep west slopes and in the narrow side valleys of the grazed area did not suffer from cowbird parasitism.

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

The current distribution of breeding success suggests the existence of a source and a sink population (Pulliam 1988; Ward & Smith 2000a). However, since both populations are immediately adjacent to each other, low dispersal abilities can be assumed to have no limiting effect on population exchange (Dunning et al. 1992; Fahrig 2001). While the differences in cowbird parasitism are intriguing, from a conservation standpoint it might be more practical to view the Pale-headed Brush-Finch as one single population in the Yunguilla Valley. Taken together, this population achieved a reproductive output of 0.74 young per pair in the year 2002, and suffered from a 38.5 % parasitism rate by Shiny Cowbirds. Depending on adult survival rates (see Chapter 1 and Krabbe, in prep.) this population may or may not be self-sustaining (Shaffer 1981; Shaffer & Samson 1985), and I conclude that cowbird parasitism is of great conservation concern. Although some species tolerate parasitism rates in excess of 50 % (Lorenzana & Sealy 1999; Smith 1999; Grzybowski & Pease 2000), isolated populations may not be self-sustaining at parasitism levels of greater than 20 % (Greene et al. 1999). It is therefore questionable whether the general threshold parasitism level of 60 % over two years suggested to justify cowbird control (Smith 1999) is applicable for the Pale-headed Brush-Finch.

4.2 Management options

A small number of bird species in North America appear to have been in a similar situation as the Pale-headed Brush-Finch, with numbers and distribution greatly reduced by loss of habitat and small isolated populations exposed to unnaturally high cowbird parasitism rates (Smith 1999; DeCapita 2000; Griffith & Griffith 2000; Hayden et al. 2000; Rothstein & Cook 2000;

Whitfield 2000). Several different approaches have been used to control parasitism rates or remove cowbirds, and the results are highly variable. The intuitively most effective cowbird removal, the killing at winter roosts or feeding sites where very large numbers congregate, has only limited applicability as a management tool (Rothstein & Robinson 1994). The high mobility of cowbirds dilutes the removal effect across the landscape, with hardly any reduction of cowbird numbers in breeding areas (Rothstein et al. 1987; Rothstein & Robinson 1994). However, in some cases the removal of large numbers of cowbirds at a regional scale proved to be more effective than a limited site-specific control program (Eckrich et al. 1999; Hayden et al. 2000).

Removal of large numbers of cowbirds is generally achieved with large cage traps, using live birds as bait (Hall & Rothstein 1999; Rothstein & Cook 2000). This is widely acknowledged to be the most effective means of cowbird control, as long as traps are placed sufficiently close to each other (Hall & Rothstein 1999; Whitfield et al. 1999; Griffith & Griffith 2000). Selective shooting has been applied to remove cowbirds at specific sites of conservation concern, however, with 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 closely monitor nests and remove cowbird eggs and chicks. While being intrusive and requiring a considerable level of skill (Griffith & Griffith 2000), nest manipulation has been demonstrated to be efficient and cost-effective, especially in remote areas where trapping is impractical (Winter & McKelvey 1999; Kus 2002).

Despite cowbird removal often leading to reduced parasitism rates, it has on only a few occasions evidently triggered an increase in the target host population (Griffith & Griffith 2000). In some cases, nesting success remained equally low, suggesting that nest predation can compensate for reduced parasitism levels (Stutchbury 1997; Schmidt & Whelan 1999; Grzybowski & Pease 2000). While the halt of a negative population trend can already be regarded as a success for endangered species, the failure of some host populations to increase despite intensive cowbird management suggests that habitat quality or quantity might be more limiting than cowbird parasitism rates alone (DeCapita 2000).

Furthermore, cowbird populations at a regional level were not affected by long-term and large-scale removal programs (DeCapita 2000; Hayden et al. 2000; Rothstein & Cook 2000).

All authors reporting from management programs stress the infinite nature of cowbird control, and it is believed to be a temporary relief for host populations without removing the causes for declining populations (Hall & Rothstein 1999; DeCapita 2000; Griffith & Griffith 2000; Hayden et al. 2000; Rothstein & Cook 2000; Whitfield 2000). Cowbird control should therefore not be regarded as the only management tool to protect a species, but should always be accompanied by habitat restoration (Griffith & Griffith 2000). This is equally valid for the Pale-headed Brush-Finch, and the search for new potential or restorable habitat should receive appropriate attention (Chapter 2).

A mandatory requirement essential to assess the efficacy of cowbird control are solid scientific baseline data (Hall & Rothstein 1999). Due to the inherent variability of host-parasite interactions, results from a single field season might not provide a basis sufficient for management decisions. To combine the possibility of taking immediate action with the need of confirming parasitism patterns found in this one-year study, I recommend an intensive monitoring program for the Pale-headed Brush-Finch in the following breeding season. While variables that might explain parasitism can be recorded at parasitized and un-parasitized nests, nest manipulation would have an equal effect as shooting of cowbirds to minimize the impact of brood parasitism. This approach would enable to collect more data on the distribution and causes of cowbird parasitism in the Yunguilla Valley, but still help to increase the reproductive output of the Pale-headed Brush-Finch. After sufficient data have been collected, the operation of several live traps within the reserve during the breeding season, and the re-introduction of extensive grazing appear to be most promising to mediate the adverse effects of cowbird parasitism on the Pale-headed Brush-Finch.

5. ACKNOWLEDGEMENTS

The study was funded by the German Academic Foreign Exchange Service (DAAD), grant number 332404010, by the Sweden Club 300 and by the Royal Society for the Protection of Birds. I am grateful to F. Sornoza (Fundacion Jocotoco), H. M. Schaefer and V. Schmidt for organizing the project and granting access to the study area. C. Wickert and J. Heathcote assisted me with nest searches and monitoring. The work benefited from correspondence with N. Krabbe, F. Bairlein and B. Schröder. The manuscript was improved by helpful comments of B. Schröder, H. M. Schaefer, V. Schmidt, and F. Bairlein.

6. REFERENCES

- Agreda, A., N. Krabbe, and O. Rodriguez. 1999. Pale-headed Brushfinch *Atlapetes pallidiceps* is not extinct. *Cotinga* **11**:50-54.
- Ammon, E. M., and P. B. Stacey. 1997. Avian nest success in relation to past grazing regimes in a montane riparian system. *Condor* **99**:7-13.
- Anderson, W. L., and R. W. Storer. 1976. Factors influencing Kirtland's Warbler nesting success. *Jack-Pine Warbler* **54**:105-115.
- Baltz, M. E. 1995. First records of the Shiny Cowbird (*Molothrus bonariensis*) in the Bahama Archipelago. *Auk* **112**:1039-1040.
- Barber, D. R., and T. E. Martin. 1997. Influence of alternate host densities in Brown-headed Cowbird parasitism rates in Black-capped Vireos. *Condor* **99**:595-604.
- BirdLife International 2000. Threatened birds of the world. Lynx Edition and BirdLife International, Barcelona and Cambridge.
- Bossuyt, B., G. Dercon, B. D. Bièvre, F. Cisneros, and J. Deckers. 1997. Agro-ecological zoning of the Austro Ecuatoriano. *The Land* **1**:159-170.
- Bradbury, R. B., A. Kyrhos, A. J. Morris, S. C. Clark, A. J. Perkins, and J. D. Wilson. 2000. Habitat associations and breeding success of yellowhammers on lowland farmland. *Journal of Applied Ecology* **37**:789-805.
- Brittingham, M. C., and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? *BioScience* **33**:31-35.
- Brittingham, M. C., and S. A. Temple. 1996. Vegetation around parasitized and non-parasitized nests within a deciduous forest. *Journal of Field Ornithology* **67**:406-413.
- Burhans, D. E. 1997. Habitat and microhabitat features associated with cowbird parasitism in two forest edge cowbird hosts. *Condor* **99**:866-872.
- Carlos, B., and F. Sornoza. 2001. Report on new population of *Atlapetes pallidiceps* discovered. Pages 1-3. Fundacion Jocotoco, Quito.
- Clotfelter, E. D. 1998. What cues do Brown-headed Cowbirds use to locate Red-winged Blackbird host nests. *Animal Behaviour* **55**:1181-1189.
- Coker, D. R., and D. E. Capen. 1995. Landscape-level habitat use by Brown-headed Cowbirds in Vermont. *Journal of Wildlife Management* **59**:631-637.
- Collar, N. J., L. P. Gonzaga, N. Krabbe, A. M. Nieto, L. G. Naranjo, T. A. Parker, and D. C. Wege 1992. Threatened birds of the Americas. International Council for Bird Preservation, Cambridge.

- Cruz, A., T. H. Manolis, and R. W. Andrews. 1995. History of Shiny Cowbird *Molothrus bonariensis* brood parasitism in Trinidad and Tobago. *Ibis* **137**:317-321.
- Curson, D. R. 1996. Nest predation and brood-parasitism of passerine birds in pinyon-juniper woodland in northeast New Mexico. MSc Thesis, University of Wisconsin, Madison.
- Dearborn, D. C. 1996. Video documentation of a Brown-headed Cowbird nestling ejecting an Indigo Bunting nestling from the nest. *Condor* **98**:645-649.
- Dearborn, D. C. 1998. Begging behavior and food acquisition by Brown-headed Cowbird nestlings. *Behavioral Ecology and Sociobiology* **43**:259-270.
- DeCapita, M. E. 2000. Brown-headed Cowbird control on Kirtland's Warbler nesting areas in Michigan. Pages 333-341 in J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. *Ecology and management of cowbirds and their hosts*. University of Texas Press, Austin.
- Dercon, G., B. Bossuyt, B. D. Bièvre, F. Cisneros, and J. Deckers 1998. Zonificación agroecológica del Austro Ecuatoriano. Promas, Universidad de Cuenca, Cuenca, Ecuador.
- Dobkin, D. S., A. C. Rich, and W. H. Pyle. 1998. Habitat and avifaunal recovery from livestock grazing in a riparian meadow system of the Northwestern Great Basin. *Conservation Biology* **12**:209-221.
- Donovan, T. M., F. R. Thompson III, and J. R. Faaborg. 2000. Cowbird distribution at different scales of fragmentation: trade-offs between breeding and feeding opportunities. Pages 255-264 in J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. *Ecology and management of cowbirds and their hosts*. University of Texas Press, Austin.
- Dufty, A. M. 2000. Cowbird brood parasitism on a little-used host: the Yellow-headed Blackbird. Pages 115-119 in J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. *Ecology and management of cowbirds and their hosts*. University of Texas Press, Austin.
- Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* **65**:169-175.
- Eckrich, G. H., T. E. Koloszar, and M. D. Goering. 1999. Effective landscape management of Brown-headed Cowbirds at Fort Hood, Texas. *Studies in Avian Biology* **18**:267-274.
- Esely, J. D., and K. D. Bollinger. 2001. Habitat selection and reproductive success of loggerhead shrikes in northwest Missouri: A hierarchical approach. *Wilson Bulletin* **113**:290-296.

- Fahrig, L. 2001. How much habitat is enough? *Biological Conservation* **100**:65-74.
- Fraga, R. M. 2002. Notes on new or rarely reported Shiny Cowbird hosts from Argentina. *Journal of Field Ornithology* **73**:213-219.
- Freeman, S. D., F. Fori, and S. Rohwer. 1990. Red-winged Blackbirds and Brown-headed Cowbirds: some aspects of a host-parasite relationship. *Condor* **92**:336-340.
- Fulton, J. T. 1990. The Shiny Cowbird (*Molothrus bonariensis*) reaches Alabama. *Alabama Birdlife* **37**:1-3.
- Gates, S., and P. F. Donald. 2000. Local extinction of British farmland birds and the prediction of further loss. *Journal of Applied Ecology* **37**:806-820.
- Goguen, C. B., and N. E. Mathews. 1998. Songbird community composition and nesting success in grazed and ungrazed pinyon-juniper woodlands. *Journal of Wildlife Management* **62**:474-484.
- Goguen, C. B., and N. E. Mathews. 1999. Review of the causes and implications of the association between cowbirds and livestock. *Studies in Avian Biology* **18**:10-17.
- Granfors, D. A., P. J. Pietz, and L. A. Joyal. 2001. Frequency of egg and nestling destruction by female Brown-headed Cowbirds at grassland nests. *Auk* **118**:765-769.
- Greene, E., J. Jolivet, and R. Redmond. 1999. Lazuli Buntings and Brown-headed Cowbirds in Montana: a state-wide landscape analysis of potential sources and sinks. *Studies in Avian Biology* **18**:135-143.
- Griffith, J. T., and J. C. Griffith. 2000. Cowbird control and the endangered Least Bell's Vireo: a management success story. Pages 342-357 in J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. *Ecology and management of cowbirds and their hosts*. University of Texas Press, Austin.
- Grzybowski, J. A., and C. M. Pease. 2000. Comparing the relative effects of brood parasitism and nest predation on seasonal fecundity in passerine birds. Pages 145-156 in J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. *Ecology and management of cowbirds and their hosts*. University of Texas Press, Austin.
- Hahn, D. C., and J. S. Hatfield. 1995. Parasitism at the landscape scale: cowbirds prefer forests. *Conservation Biology* **9**:1415-1424.
- Hall, L. S., and S. I. Rothstein. 1999. Cowbird control: the efficacy of long-term control and proposed alternatives to standard control practices. *Studies in Avian Biology* **18**:254-259.
- Hauber, M. E., and S. A. Russo. 2000. Perch proximity correlates with higher rates of cowbird parasitism of ground nesting song sparrows. *Wilson Bulletin* **112**:150-153.

- Hayden, T. J., D. J. Tazik, R. H. Melton, and J. D. Cornelius. 2000. Cowbird control program at Fort Hood, Texas: lessons for mitigation of cowbird parasitism on a landscape scale. Pages 357-370 in J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. Ecology and management of cowbirds and their hosts. University of Texas Press, Austin.
- Johnsgard, P. A. 1997. The avian brood parasites. Oxford University Press, New York.
- Kluza, D. A. 1998. First record of Shiny Cowbird (*Molothrus bonariensis*) in Yucatán, Mexico. Wilson Bulletin **110**:429-430.
- Krabbe, N. in prep. Pale-headed Brush-Finch *Atlapetes pallidiceps* (Aves: Emberizidae): Notes on population size, habitat, vocalizations, feeding, interference competition, and conservation.
- Kus, B. E. 2002. Fitness consequences of nest desertion in an endangered host, the Least Bell's Vireo. Condor **104**:795-802.
- Larison, B., S. A. Laymon, P. L. Williams, and T. B. Smith. 1998. Song Sparrows vs. cowbird brood parasites: impacts of forest structure and nest-site selection. Condor **100**:93-101.
- Larison, B., S. A. Laymon, P. L. Williams, and T. B. Smith. 2001. Avian responses to restoration: nest site selection and reproductive success in Song Sparrows. Auk **118**:432-442.
- Lichtenstein, G., and S. G. Sealy. 1998. Nestling competition, rather than supernormal stimulus, explains the success of parasitic brown-headed cowbird chicks in yellow warbler nests. Proceedings of the Royal Society of London B **265**:249-254.
- Lorenzana, J. C., and S. G. Sealy. 1999. A meta-analysis of the impact of parasitism by the Brown-headed Cowbird on its hosts. Studies in Avian Biology **18**:241-253.
- Marin, M. 2000. The Shiny Cowbird (*Molothrus bonariensis*) in Chile: introduction or dispersion? Its hosts and parasitic trends. Ornitologia Neotropical **11**:285-296.
- Martin, T. E., and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology **64**:507-519.
- Massoni, V., and J. C. Reboresda. 2002. A neglected cost of brood parasitism: egg punctures by Shiny Cowbirds during inspection of potential host nests. Condor **104**:407-412.
- McLaren, C. M., and S. G. Sealy. 2000. Are nest predation and brood parasitism correlated in Yellow Warblers? A test of the cowbird predation hypothesis. Auk **117**:1056-1060.
- Payne, R. B. 1997. Avian brood parasitism. Pages 338-369 in D. H. Clayton, and J. Moore, editors. Host-Parasite evolution: general principles and avian models. Oxford University Press, New York.

- Peterjohn, B. G., J. R. Sauer, and S. Schwarz. 2000. Temporal and geographic patterns in population trends of Brown-headed Cowbirds. Pages 21-34 in J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. Ecology and management of cowbirds and their hosts. University of Texas Press, Austin.
- Petit, L. J., and D. R. Petit. 2000. Brown-headed Cowbird parasitism of migratory birds: effects of forest area and surrounding landscape. Pages 265-270 in J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. Ecology and management of cowbirds and their hosts. University of Texas Press, Austin.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* **132**:652-661.
- Robinson, S. K., J. D. Brawn, S. F. Morse, and J. R. Herkert. 1999. Use of different habitats by breeding Brown-headed Cowbirds in fragmented western landscapes. *Studies in Avian Biology* **18**:52-61.
- Rodewald, A. D., and R. H. Yahner. 2001. Avian nesting success in forested landscapes: influence of landscape composition, stand and nest-patch microhabitat, and biotic interactions. *Auk* **118**:1018-1028.
- Rothstein, S. I., and T. L. Cook. 2000. Cowbird management, host population limitation, and efforts to save endangered species - Introduction. Pages 323-332 in J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. Ecology and management of cowbirds and their hosts. University of Texas Press, Austin.
- Rothstein, S. I., and S. K. Robinson. 1994. Conservation and coevolutionary implications of brood parasitism by cowbirds. *Trends in Ecology and Evolution* **9**:162-164.
- Rothstein, S. I., and S. K. Robinson. 2000. Population trends of cowbirds and hosts and relevant methodology - Introduction. Pages 13-20 in J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. Ecology and management of cowbirds and their hosts. University of Texas Press, Austin.
- Rothstein, S. I., J. Verner, E. Stevens, and L. V. Ritter. 1987. Behavioral differences among sex and age classes of the Brown-headed Cowbird and their relation to the efficacy of a control program. *Wilson Bulletin* **99**:322-337.
- Schmidt, K. A., and C. J. Whelan. 1999. The relative impacts of nest predation and brood parasitism on seasonal fecundity in songbirds. *Conservation Biology* **13**:46-57.
- Shaffer, M. L. 1981. Minimum population sizes for species conservation. *BioScience* **31**:131-134.

- Shaffer, M. L., and F. B. Samson. 1985. Population size and extinction: a note on determining critical population sizes. *American Naturalist* **125**:144-152.
- Smith, J. N. M. 1999. The basis for cowbird management: host selection, impacts on hosts, and criteria for taking management action. *Studies in Avian Biology* **18**:104-108.
- Smith, J. N. M., and S. I. Rothstein. 2000. Brown-headed Cowbirds as a model system for studies of behavior, ecology, evolution, and conservation biology. Pages 1-9 in J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. *Ecology and management of cowbirds and their hosts*. University of Texas Press, Austin.
- Staab, C. A., and M. L. Morrison. 1999. Managing riparian vegetation to control cowbirds. *Studies in Avian Biology* **18**:18-22.
- Strausberger, B. M. 2001. The relationship of habitat and spatial distribution of nests with Brown-headed Cowbird parasitism of Red-winged Blackbirds. *Wilson Bulletin* **113**:129-261.
- Stutchbury, B. J. M. 1997. Effects of female cowbird removal on reproductive success of Hooded Warblers. *Wilson Bulletin* **109**:74-81.
- Taylor, D. M. 1986. Effects of cattle grazing on passerine birds nesting in riparian habitat. *Journal of Range Management* **39**:254-258.
- Tewksbury, J. J., T. E. Martin, S. J. Hejl, T. S. Redman, and F. J. Wheeler. 1999. Cowbirds in a western valley: effects of landscape structure, vegetation, and host density. *Studies in Avian Biology* **18**:23-33.
- Uyehara, J. C., and M. J. Whitfield. 2000. Association of cowbird parasitism and vegetative cover in territories of southwestern Willow Flycatchers. Pages 204-209 in J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. *Ecology and management of cowbirds and their hosts*. University of Texas Press, Austin.
- Ward, D., and J. N. M. Smith. 2000a. Brown-headed Cowbird parasitism results in a sink population in Warbling Vireos. *Auk* **117**:337-344.
- Ward, D., and J. N. M. Smith. 2000b. Interhabitat differences in parasitism frequencies by Brown-headed Cowbirds in the Okanagan Valley, British Columbia. Pages 210-219 in J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. *Ecology and management of cowbirds and their hosts*. University of Texas Press, Austin.
- Whitfield, M. J. 2000. Results of a Brown-headed Cowbird control program for the southwestern Willow Flycatcher. Pages 371-377 in J. N. M. Smith, T. L. Cook, S. I.

- Rothstein, S. K. Robinson, and S. G. Sealy, editors. Ecology and management of cowbirds and their hosts. University of Texas Press, Austin.
- Whitfield, M. J., K. M. Enos, and S. P. Rowe. 1999. Is Brown-headed Cowbird trapping effective for managing populations of the endangered Southwestern Willow Flycatcher? *Studies in Avian Biology* **18**:260-266.
- Winter, K. J., and S. D. McKelvey. 1999. Cowbird trapping in remote areas: alternative control measures may be more effective. *Studies in Avian Biology* **18**:282-289.
- Wood, D. R., and E. K. Bollinger. 1997. Egg removal by Brown-headed Cowbirds: a field test of the host incubation efficiency hypothesis. *Condor* **99**:851-857.
- Young, J. S., and R. L. Hutto. 1999. Habitat and landscape factors affecting cowbird distribution in the northern Rockies. *Studies in Avian Biology* **18**:41-51.

SYNOPSIS

In 1986, D. H. Janzen reflected about the loss of biodiversity, and stated with reference to small and localized endemic populations that „in much of the Neotropics, what we call endangered is for the most part already extinct. (...) These are the living dead“ (Janzen 1986).

Whether this fate will be true for the Pale-headed Brush-Finch, who meets all the criteria that typically render a species vulnerable to stochastic extinction, remains to be seen. Here, I will summarize the major findings presented in the previous chapters, and make an attempt to evaluate the odds against which the small remnant population of the Pale-headed Brush-Finch stands.

Bird species have all over the world declined due to anthropogenic landscape modification and an increasing fragmentation of the remaining suitable habitats (Bradbury et al. 2000; Chamberlain et al. 2000; Gates & Donald 2000; Ford et al. 2001). The Pale-headed Brush-Finch, too, is strongly affected by the landscape destruction in its limited geographic range in southern Ecuador both directly and indirectly. The loss of habitat has probably caused the decline of this species, and will due to its often irreversible effects limit the current population to a few sheltered places in the future. This direct effect might have become recently accelerated by increasing levels of brood parasitism by Shiny Cowbirds, even though data are lacking to what extend the Pale-headed Brush-Finch might have been exposed to brood parasitism in its natural habitat.

Which of the factors is worse and deserves immediate attention and management? Assuming the remaining habitat in which the Pale-headed Brush-Finch still persists is suitable, the population should not be immediately threatened with extinction, given the habitat does not deteriorate. However, if cowbird parasitism prevents successful reproduction, this small population will hardly be able to sustain itself. Similar patterns from restricted range species in North America, most notably the Kirtland`s Warbler (*Dendroica kirtlandii*), suggest that cowbird parasitism would

have eliminated this species if not controlling measures had been initiated (Rothstein & Cook 2000).

The threat that cowbird parasitism causes for the Pale-headed Brush-Finch might be even stronger due to the observed single-broodedness of the species. While many species suffer only partial losses due to brood parasitism, the successful raising of a cowbird fledgling will likely result in a total loss of reproductive output for a Pale-headed Brush-Finch. Mixed broods seem to be rare, a second clutch is not initiated, and the birds continue to feed “their” offspring for the remaining season. Egg rejection could not be confirmed in this study, and it seems as if the Pale-headed Brush-Finch has only very limited defense mechanisms towards cowbird parasitism. This has often been assumed to be a result of evolutionary lag in species that became only recently exposed to cowbird parasitism (Rothstein & Robinson 1994; Takasu 1998; Hosoi & Rothstein 2000; Rothstein 2001). But why should it apply to the Pale-headed Brush-Finch, who occurs in the center of the Shiny Cowbird’s natural range and has therefore likely co-existed with the Shiny Cowbird for a long time? Here again, the uncertainty of the natural habitat of the Pale-headed Brush-Finch precludes conclusive considerations. In Chapter Two I discussed the possibility that the Pale-headed Brush-Finch might have naturally occurred on landslides and other regenerating patches within contiguous forest tracts. These openings are less frequented by cowbirds than the large scale “openings” provided by farmland (Coker & Capen 1995). Naturally small parasitism levels might have prevented the evolution of defense mechanisms, when the costs did not outweigh the benefits (Brooke & Davies 1987). Cowbirds tend to exhibit affinities to livestock (Goguen & Mathews 1999), and the provisioning of food resources through agricultural practices is generally believed to have supported cowbirds (Brittingham & Temple 1983; Rothstein & Robinson 1994). It is therefore very likely that human influence in the Rio Jubones drainage has greatly altered the extent to which the Pale-headed Brush-Finch is exposed to brood parasitism by Shiny Cowbirds. Consequently, an attempt to minimize the impact of cowbirds on the reproductive output of the Pale-headed Brush-Finch appears to be a legitimate approach.

In Chapter Three I have outlined some of the options available for the management of cowbirds. While immediate action seems prudent to prevent any further losses of reproductive output of the Pale-headed Brush-Finch, this has to be weighed against the loss of information that will result from a control program modifying a still largely unstudied system. Adaptive management is very popular among conservation managers, but it often precludes improved understanding of a system and the actual effects of management practices (Simberloff 1998). The proposed commencement of shooting of cowbirds within the reserve (Krabbe in prep.) has to be critically viewed in the light of naturally variable reproductive rates and alternative options. The year 2002 deviates from the general population trends (see below) in having an exceptionally low breeding success (Krabbe in prep.). This implies that at least another year of data collection is required to found management decisions on a solid basis. It should, however, be combined with nest manipulation, thereby reducing the impact of cowbirds but maintaining the potential for scientific investigations.

If cowbird management will eventually turn out to be the last resort to save the Pale-headed Brush-Finch, then much more rigorous practices might have to be employed. Shooting has proven ineffective in many North American studies, and it is unlikely that Shiny Cowbirds will respond differently to Brown-headed Cowbirds. The breeding area home range of a female Shiny Cowbird is estimated to be at least 4 km² (Johnsgard 1997), and the high fecundity of Shiny Cowbirds (Kattan 1997) could result in a single female potentially parasitizing the entire population of the Pale-headed Brush-Finch! An integrated approach using traps, complementary shooting, and nest manipulation might turn out to be necessary. The Pale-headed Brush-Finch could then fall victim to the lack of financial resources, when funding cannot keep up the required life-sustaining measures.

As studies from North America show, an increase of the population size is not guaranteed even with efficient cowbird removal programs. Cowbird control alone is unlikely to be an alleviating panacea for the Pale-headed Brush-Finch. The identification and restoration of more suitable habitat is therefore of equal importance as the selection of the most useful cowbird management practice. I have pointed out in Chapter One that small populations might remain in seemingly suitable habitat patches in the region, and future search effort should focus on the

patches that match the criteria identified as important in the habitat use analysis. A mosaic of low dense scrub and grassy clearings appears to be the most suitable habitat at present. Furthermore, the availability of overhanging bamboo or herbaceous vines for the placement of nests less vulnerable to predation might be a factor not yet considered in previous searches. The influence of predation could not be quantified in this study, but, as briefly mentioned in Chapter Three, might have considerable effects on the reproductive success of the Pale-headed Brush-Finch. Predators are known to be generally more abundant in edge habitat and therefore often exert strongest influences in small habitat fragments with a high edge-to-area ratio (Andrén & Angelstam 1988; Marini et al. 1995; Carlson & Hartman 2001; Lahti 2001). Krabbe (in prep.) explained his failure to find further populations of the Pale-headed Brush-Finch with the small size of remaining potential habitat fragments. Local extinction of the Pale-headed Brush-Finch in these places could have been caused by cowbird parasitism or environmental stochasticity.

Small habitat fragments that provide insufficient resources for a self-sustaining population can persist when mortality is compensated by immigration (Pulliam 1988; Reich & Grimm 1996). Another important aspect of conservation relevance is therefore to what extent the Pale-headed Brush-Finch has the ability to disperse and re-colonize suitable habitat. Fragmentation of the landscape is well known to adversely affect the movements of birds and other animals (Gibbs 1998; Belisle & Desrochers 2002; Pattanavibool & Dearden 2002). Since the natural environment of the Pale-headed Brush-Finch is unknown, its sensitivity to fragmentation is difficult to estimate. Further research is required to determine the dispersal and colonizing abilities of the Pale-headed Brush-Finch, in order to ascertain whether adequate stepping stones or connecting corridors may have to be provided.

Demographic effects are not solely determined by environmental influences, but also inherently depend on the life-history of the species. The results of this study indicate that the Pale-headed Brush-Finch exhibits features of a k-selected species. If only one brood is raised per year, and a maximum of three chicks can be raised in one clutch, then the annual reproductive output is low compared to similar sized passerines. This might be an adaptation to reduced adult mortality and longer life spans (Martin et al. 2000). However, this hypothesis is undermined by the annual turnover rate of singing males, which has been estimated to lie between 30-40 % in

the Yunguilla reserve (Krabbe in prep.). This would mean that the population would completely replace itself within 2-3 years, and would require either a higher reproductive output or very low juvenile mortality. Again, more intensive research is required to clarify the life-history traits of the Pale-headed Brush-Finch.

Recent population development has been slightly positive, with the population increasing from 10 to 17 singing males within the reserve over the last four years, yielding a total population number of 37 territories in 2002 (Krabbe in prep.). Whether this trend will be reversed by increasing brood parasitism rates is one of the most interesting questions of the near future. Local extinctions that resulted from indirect effects from the surrounding environment are often slow and blurred (Woinarski & Wykes 1983; Brooks et al. 1999). For the Pale-headed Brush-Finch, this last local extinction would be fatal, and a large effort should be made to help this species disprove Janzen's (1986) terminology.

References

- Andr n, H., and P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. *Ecology* **69**:544-547.
- Belisle, M., and A. Desrochers. 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. *Landscape Ecology* **17**:219-231.
- Bradbury, R. B., A. Kyrhos, A. J. Morris, S. C. Clark, A. J. Perkins, and J. D. Wilson. 2000. Habitat associations and breeding success of yellowhammers on lowland farmland. *Journal of Applied Ecology* **37**:789-805.
- Brittingham, M. C., and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? *BioScience* **33**:31-35.
- Brooke, M. d. L., and N. B. Davies. 1987. Recent changes in host use by cuckoos *Cuculus canorus* in Britain. *Journal of Animal Ecology* **56**:873-883.
- Brooks, T. M., S. L. Pimm, and J. O. Oyugi. 1999. Time lag between deforestation and bird extinction in tropical forest fragments. *Conservation Biology* **13**:1140-1150.

- Carlson, A., and G. Hartman. 2001. Tropical forest fragmentation and nest predation - an experimental study in Eastern Arc montane forest, Tanzania. *Biodiversity and Conservation* **10**:1077-1085.
- Chamberlain, D. E., R. J. Fuller, R. G. H. Bunce, J. C. Duckworth, and M. Shrubbs. 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *Journal of Applied Ecology* **37**:771-788.
- Coker, D. R., and D. E. Capen. 1995. Landscape-level habitat use by Brown-headed Cowbirds in Vermont. *Journal of Wildlife Management* **59**:631-637.
- Ford, H. A., G. W. Barrett, D. A. Saunders, and H. F. Recher. 2001. Why have birds in the woodlands of Southern Australia declined? *Biological Conservation* **97**:71-88.
- Gates, S., and P. F. Donald. 2000. Local extinction of British farmland birds and the prediction of further loss. *Journal of Applied Ecology* **37**:806-820.
- Gibbs, J. P. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. *Landscape Ecology* **13**:263-268.
- Goguen, C. B., and N. E. Mathews. 1999. Review of the causes and implications of the association between cowbirds and livestock. *Studies in Avian Biology* **18**:10-17.
- Hosoi, S. A., and S. I. Rothstein. 2000. Nest desertion and cowbird parasitism: evidence for evolved responses and evolutionary lag. *Animal Behaviour* **59**:823-840.
- Janzen, D. 1986. Blurry catastrophes. *Oikos* **47**:1-2.
- Johnsgard, P. A. 1997. *The avian brood parasites*. Oxford University Press, New York.
- Kattan, G. H. 1997. Shiny cowbirds follow the `shotgun` strategy of brood parasitism. *Animal Behaviour* **53**:647-654.
- Krabbe, N. in prep. Pale-headed Brush-Finch *Atlapetes pallidiceps* (Aves: Emberizidae): Notes on population size, habitat, vocalizations, feeding, interference competition, and conservation.
- Lahti, D. C. 2001. The "edge effect on nest predation" hypothesis after twenty years. *Biological Conservation* **99**:365-374.

- Marini, M. A., S. K. Robinson, and E. J. Heske. 1995. Edge effects on nest predation in the Shawnee National Forest, southern Illinois. *Biological Conservation* **74**:203-213.
- Martin, T. E., P. R. Martin, C. R. Olson, B. J. Heidinger, and J. J. Fontaine. 2000. Parental care and clutch sizes in North and South American birds. *Science* **287**:1482-1485.
- Pattanavibool, A., and P. Dearden. 2002. Fragmentation and wildlife in montane evergreen forests of northern Thailand. *Biological Conservation* **107**:155-164.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* **132**:652-661.
- Reich, M., and V. Grimm. 1996. Das Metapopulationskonzept in Ökologie und Naturschutz: Eine kritische Bestandsaufnahme. *Zeitschrift für Ökologie und Naturschutz* **5**:123-139.
- Rothstein, S. I. 2001. Relic behaviours, coevolution and the retention versus loss of host defences after episodes of avian brood parasitism. *Animal Behaviour* **61**:95-107.
- Rothstein, S. I., and T. L. Cook. 2000. Cowbird management, host population limitation, and efforts to save endangered species - Introduction. Pages 323-332 in S. G. Sealy, editor. *Ecology and management of cowbirds and their hosts*. University of Texas Press, Austin.
- Rothstein, S. I., and S. K. Robinson. 1994. Conservation and coevolutionary implications of brood parasitism by cowbirds. *Trends in Ecology and Evolution* **9**:162-164.
- Simberloff, D. 1998. Flagships, umbrellas and keystones: is single-species management passé in the landscape era? *Biological Conservation* **83**:247-257.
- Takasu, F. 1998. Modelling the arms race in avian brood parasitism. *Evolutionary Ecology* **12**:969-987.
- Woinarski, J. C. Z., and B. J. Wykes. 1983. Decline and extinction of the Helmeted Honeyeater at Cardinia Creek. *Biological Conservation* **27**:7-21.