

Habitat selection by the pale-headed brush-finch (*Atlapetes pallidiceps*) in southern Ecuador: implications for conservation

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Abstract

The pale-headed brush-finch (*Atlapetes pallidiceps*) is threatened with extinction due to habitat loss, but very little is known about its ecological requirements. We used multiple logistic regression to study habitat selection of this species at landscape, territory, and nest site scales in order to make recommendations about effective management. Habitat selection by the sympatric stripe-headed brush-finch (*Buarremon torquatus*) was examined with the same methods in order to analyse interspecific resource partitioning and potential competition. The pale-headed brush-finch selected semi-open habitat types with intermediate scrub heights, and avoided forests. Nest sites depended on the presence of vines or bamboo. By contrast, the stripe-headed brush-finch chose dense habitat with low ground cover under tall vegetation and avoided semi-open habitat. The two species had overlapping territories but differed significantly in microhabitat use and the use of vegetation strata. We found no convincing evidence that the stripe-headed brush-finch displaces the pale-headed brush-finch from optimal habitat. The preservation of semi-open scrubland maintained by low-intensity grazing is suggested for future conservation of the pale-headed brush-finch.

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1. Introduction

Knowledge of a species' ecological requirements is a prerequisite for successful conservation (Austin et al., 1996; Araújo et al., 2002; Luck, 2002). Especially in the tropics, where anthropogenic landscape modifications rapidly reduce many natural habitats, the lack of detailed biological knowledge handicaps effective conservation of many rare species. One of several critically endangered bird species in the tropics whose habitat preferences are little known is the pale-headed brush-finch (*Atlapetes pallidiceps*) (BirdLife International, 2000). The species went unrecorded for 30 years and was re-discovered in 1998 (Agreda et al., 1999). It is endemic to a single valley in the Andes of southern Ecuador (Paynter, 1972; Collar et al., 1992; Ridgely and Greenfield, 2001), and its total population is currently esti-

mated at ca. 35 breeding pairs (Sornoza and Krabbe, pers. comm.). At the site of this last remnant population, vegetation is changing rapidly due to natural succession, and management is needed to sustain suitable habitat (Agreda et al., 1999). This requires an understanding of the species' habitat preferences that can best be provided by quantitative exploration of its resource use patterns.

The specific objectives of this study were to: (1) determine factors that influence the distribution of the pale-headed brush-finch at the landscape scale, (2) analyse habitat selection within territories, (3) characterize nest site selection, and (4) assess implications of the findings for the conservation of the pale-headed brush-finch.

Interspecific competition is assumed to be an important factor governing bird distributions in the Andes (Haffer, 1967; Terborgh and Weske, 1975; Fjeldså and Krabbe, 1990; Remsen and Graves, 1995a,b). The only currently known population of the pale-headed brush-finch co-occurs with the stripe-headed brush-finch (*Buarremon torquatus*), a widely distributed bird of dense moist undergrowth and forest borders from the

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upper tropical to the temperate zone (Paynter, 1978; Remsen and Graves, 1995b; Ridgely and Greenfield, 2001). Concern has been raised that this species might compete with, and displace the pale-headed brush-finch from optimal habitat (Agrega et al., 1999; Krabbe, pers. comm.). Both Paynter (1978) and Remsen and Graves (1995a,b) noted that sympatrically occurring brush-finch species differ in microhabitat use. However, Remsen and Graves (1995b) could not resolve the role of interspecific competition as a determinant of distribution patterns. In this study, we analysed the habitat use and small-scale distribution of both species, and tried to determine whether they exhibit interspecific territoriality. We then compared microhabitat use of both species in order to test whether differing habitat preferences can account for resource partitioning and thus enable coexistence.

2. Methods

2.1. Study area

The study area is located in Yunguilla Valley, ca. 50 km southwest of Cuenca in Province Azuay, Ecuador (3°13'S; 79°16'W). It is 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). The region is intensively farmed, with corn crops and cattle pastures being the dominant forms of land-use (Bossuyt et al., 1997; Dercon et al., 1998).

The site where *A. pallidiceps* was rediscovered in 1998 (Agrega et al., 1999) encompasses two steep (ca. 45°) slopes with an area of ca. 80 ha, ranging from 1650 to 2100 m in altitude. It has been declared a reserve and is largely ungrazed. A subsequently discovered population on the neighbouring hill inhabits an equally large area that is still grazed by cattle (Sornoza, pers. comm.). Both hills feature semi-open habitats with patches of dense arid scrub consisting mostly of composite and verbenaceous species, interspersed with grassland of old or recent pastures. Small stands of *Acacia* sp. and lauraceous trees are found in more humid parts, and fragments of semi-humid forest persist on western and southern slopes. Large patches of dwarf bamboo (*Chusquea* sp.) occur in small depressions, ravines, and on the more humid western slopes. The arid scrub is deciduous and sheds its leaves during the dry season from June to September, whereas bamboo retains its leaves throughout the year.

2.2. Point sampling

Birds were monitored from dawn to early afternoon every day between late March and mid-June 2002. For

every independent sighting of *A. pallidiceps* or *B. torquatus*, we recorded the following variables in an estimated circle of 5 m radius around the perch site: aspect; inclination (1 = 0–20°, 2 = 21–40°, 3 = >40°); vegetation density (1 = open, 2 = semi-open, 3 = open scrub with visibility >10 m, 4 = dense scrub with visibility 5–10 m, 5 = dense scrub with visibility <5 m); cover of vines (1 = 0–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, 5 = 81–100%); bush, tree, and grass cover, as well as cover of herbaceous ground vegetation (all in %); bamboo (as % of total bush cover); maximum and most common vegetation height (height of the tallest and height of the majority of plants, hereafter max height and modal height, respectively); and position of the bird (all in cm). If two individuals of the same species simultaneously perched <5 m apart, habitat parameters were averaged between them and the sightings were treated as a single observation. Independence of point records was assured by maintaining a 5 min time lag between consecutive observations of the same individual (Morrison, 1984; Bradley, 1985). Effective sample size was limited by the small population of *A. pallidiceps* (Machlis et al., 1985). We sampled ca. 95% of the entire population, and no individual contributed >5% to the data set.

We measured all habitat variables except bird position at 332 points that were distributed in a random pattern across the study area, in order to compare resource use with availability. Coordinates of random points were defined on a map by a random-number generator. Based on previous observations, all random points were divided into being within or outside a territory of either the *A. pallidiceps* or *B. torquatus*. Those random points that fell within known territories of a species were defined “available” to that species at the territory level, since we were not able to determine unused points for the territory scale analysis.

Nests of *A. pallidiceps* were located using standard searching techniques (Martin and Geupel, 1993; Opper, 2002), and nest sites were characterized with the same variables as above.

2.3. Model construction and statistical analysis

We compared observed positions of both species and random points using non-parametric Mann–Whitney *U* tests to examine whether brush-finches use resources in proportion to their abundance. We then used multiple logistic regression (Hosmer and Lemeshow, 2000) to analyse habitat selection at the landscape, territory, and nest site scales (cf. Orians and Wittenberger, 1991; Jones, 2001). At the landscape scale, observed points of each species (used) were compared with random habitat points outside the respective species' territories (unused). For the territory scale analysis, we compared observed points of each species with random points within the respective species' territories, with the latter representing

habitat availability (McClean et al., 1998; Jones, 2001). Nest site selection of *A. pallidiceps* was examined by comparing the habitat parameters obtained from nest sites with non-nest sites within those territories where nests were found.

Differences in microhabitat use between both brush-finch species were investigated with logistic regression, in order to determine if, and which of the measured variables contribute to ecological separation of the two species. We then analysed foraging height in more detail, by classifying the vertical positions of foraging birds into four vegetation strata; ground or near ground (0–80 cm), lower scrub stratum (81–140 cm), scrub centre (141–250 cm), and scrub canopy or trees (>250 cm). We then divided observations of *A. pallidiceps* into those with and without presence of *B. torquatus* to examine whether stratum usage differed at sites of co-occurrence. Contingency table analysis was applied to test for differences between use of strata among birds.

For the logistic regression approach we first reduced multicollinearity between variables by eliminating one of a pair of variables with a bivariate Spearman's correlation coefficient of $r_s > 0.7$ (Fielding and Haworth, 1995). Then a backward stepwise procedure was applied to determine which variables contributed significantly to models that predict the probability of occurrence (Hosmer and Lemeshow, 2000). Depending on the number of correlated variables, several models were calculated, alternatively omitting correlated variables. We used Akaike's Information Criterion (AIC) to choose the most parsimonious model that offered the highest accuracy with the least variables (Burnham and Anderson, 1992; Buckland et al., 1997; Reineking and Schröder, in press).

All models were internally validated to assess their predictive power. Models with mutually exclusive states of the dependent variable (landscape and nest site scales, interspecific comparison) were internally validated using the bootstrapping procedure (Verbyla and Litvaitis,

1989; Reineking and Schröder, in press). We improved variable selection by using the backward stepwise approach with $\alpha = 0.05$ and 300 bootstrap samples to obtain the final model. To yield realistic estimates of the predictive ability of the final model we calculated ROC-curves (Fielding and Bell, 1997; Schröder, 2000). The area under the ROC-curve (AUC) represents the model's predictive performance independent of an arbitrarily defined cut-off value (Hanley and McNeil, 1982). We describe final model performance by Nagelkerke's R^2 (Nagelkerke, 1991) and the AUC-value after the internal validation as well as an optimised correct classification rate calculated from the ROC curve (Zweig and Campbell, 1993; Schröder, 2000).

Models without mutually exclusive states of the dependent variable (territory scale) were 5-fold cross-validated to classify the accuracy of the model (Verbyla and Litvaitis, 1989). We applied the model obtained from four fifths of the full data set to the remaining one fifth of the data, and classified predicted probabilities into 10 equally spaced categories. According to Boyce et al. (2002), the model is considered accurate if the number of observations in each category is strongly positively correlated (Spearman-rank correlation $r_s > 0.7$) with the category value within the presence subset of the test data. All analyses were carried out with the statistical package SPSS 11™ and in R (1.5.1, available at <http://cran.r-project.org>), respectively.

3. Results

3.1. Landscape and territory scale

Twenty-six territories of *A. pallidiceps* were found, and 50 individuals were sampled for habitat use. They were observed in a variety of habitats ranging from dense scrub to single bushes in grassy patches. Means of all observations are listed in Table 1. The analysis of

Table 1
Details (mean \pm SD) and univariate comparison (Mann–Whitney U tests) of microhabitat use of brush-finches in Yunguilla Valley, Ecuador

Variable	<i>A. pallidiceps</i> (n = 746)	<i>B. torquatus</i> (n = 181)	z	P	Multivariate model ^a
Aspect (sin transformed)	0.55 \pm 0.58	0.55 \pm 0.57	–1.371	0.170	
Inclination (1–5)	2.44 \pm 0.64	2.08 \pm 0.69	–6.335	<0.001	
Bush cover (%)	65.90 \pm 25.54	92.79 \pm 12.02	–14.206	<0.001	
Tree cover (%)	4.50 \pm 11.20	27.51 \pm 26.76	–14.074	<0.001	–
Grass cover (%)	30.38 \pm 27.02	5.17 \pm 9.82	–13.275	<0.001	+
Herb cover (%)	18.88 \pm 16.36	23.28 \pm 18.30	–2.489	0.013	
Bamboo (%)	22.28 \pm 30.92	19.81 \pm 29.84	–1.046	0.296	+
Vines (1–5)	2.13 \pm 1.11	2.79 \pm 1.28	–6.480	<0.001	
Vegetation density (1–5)	3.10 \pm 1.05	3.93 \pm 0.93	–9.273	<0.001	–
Maximum height (cm)	461.50 \pm 175.14	777.90 \pm 334.22	–13.378	<0.001	
Model height (cm)	275.27 \pm 93.56	420.99 \pm 195.37	–11.524	<0.001	–
Position (cm)	201.33 \pm 117.87	127.43 \pm 113.50	–7.822	<0.001	+

^a Indicates the variables that were included in a logistic regression model separating the two species, symbols indicate whether likelihood of an observation belonging to *A. pallidiceps* is positively (+) or negatively (–) correlated with the variable; all variables were significant at $P \leq 0.001$.

Table 2

Univariate comparison (Mann–Whitney U tests) of habitat variables between observed points of brush-finches and random points outside (landscape scale) and within territories (territory scale) in Yunguilla Valley, Ecuador; symbols indicate whether a resource was used more (+), less (–) or in proportion (0) to abundance; + or – $P < 0.05$, ++ or – $P < 0.01$, +++ or – $P < 0.001$; details are given in Table 1; details can be obtained from the authors upon request

Variable	Landscape scale		Territory scale	
	<i>A. pallidiceps</i>	<i>B. torquatus</i>	<i>A. pallidiceps</i>	<i>B. torquatus</i>
Aspect (sin transformed)	+++	0	0	+
Inclination (1–5)	0	---	0	---
Bush cover (%)	+++	+++	0	0
Tree cover (%)	---	+++	0	+++
Grass cover (%)	---	---	0	0
Herb cover (%)	+++	+++	+++	+++
Bamboo (%)	0	--	0	+
Vines (1–5)	+++	+++	+++	+++
Vegetation density (1–5)	+++	+++	0	0
Maximum height (cm)	---	+++	+	+++
Model height (cm)	---	+++	0	0

point samples between all sightings of *A. pallidiceps* and all random points outside territories (unused points, absence) indicated that vegetation density, bush, vine and herb cover were significantly higher at used than at unused points (Table 2). By contrast, grass and tree cover were significantly lower. The maximum and modal height of the scrub was lower at used than at unused points.

The logistic regression equation indicated that the presence probability of *A. pallidiceps* increases with greater vegetation density, bush, and herb cover, and with lower tree cover as well as modal height (AIC = 546.56, $n = 822$; Table 3). The model correctly classified 88.6% of points, and internal validation did

not significantly reduce predictive success (Nagelkerke- $R^2 = 0.483$, $AUC_{bootstrapped} = 0.873$).

A. pallidiceps territories were ca. 1 ha in size. When considered at the territory scale, many resources were used in proportion to their abundance. As at the landscape scale, herb and vine cover were again greater, but maximum height was also greater at points used by *A. pallidiceps* than at available random points. Likewise, the positions of the birds were best predicted by the same variables as at the landscape scale, plus increasing bamboo and vine cover (AIC = 858.187, $n = 861$, Table 3). The model provided acceptable results in cross-validation tests, with the predicted presence being strongly positively correlated with actual presence (Spearman $r_s = 0.793$, $P < 0.01$).

B. torquatus occurred mainly in the dense scrub with good tree cover and little ground vegetation (Table 1). The observed sites had similar characteristics as for *A. pallidiceps* in comparison to unused sites, with major differences being less grass cover and taller vegetation (Table 2). At the landscape scale, maximum and modal height were on average 2–3 m higher at used points than at unused points. The analysis yielded a multiple logistic regression model that predicted increasing presence probability with greater vine cover, vegetation density and maximum vegetation height, and lower grass cover (AIC = 295.84, $n = 517$; Table 3). It correctly classified 86.7% of observations, resulting in a model performance of Nagelkerke- $R^2 = 0.672$ and $AUC_{bootstrapped} = 0.878$ after internal validation.

Some of the variables selected for at the landscape scale were also used more than was available on average at the territory scale (Table 2). For example, *B. torquatus* was observed at points that had significantly higher proportions of vine, tree and herb cover than was available at random points in territories. Maximum height was significantly greater at used than at random points, but model height was not. The logistic regression

Table 3

Summary of variables included in logistic regression models describing habitat selection of brush-finches at different spatial scales in Yunguilla Valley, Ecuador; symbols indicate whether the probability of a species being present is positively (+) or negatively (–) correlated with the variable; + or – $P < 0.05$, ++ or – $P < 0.01$, +++ or – $P < 0.001$; details can be obtained from the authors upon request

	<i>A. pallidiceps</i>	<i>B. torquatus</i>
Landscape scale	Sin-transformed aspect (+++)	Sin-transformed aspect (++)
	Vegetation density (+++)	Vegetation density (++)
	Modal height (– –)	Maximum height (+++)
	Tree cover (– – –)	Vine cover (+++)
	Bush cover (+++)	
	Herb cover (+++)	
Territory scale	Tree cover (– –)	Model failed
	Bush cover (++)	
	Herb cover (++)	
	Bamboo cover (++)	
Nest site scale	Tree cover (– –)	No data
	Bamboo cover (+++)	
	Vine cover (+++)	

model failed to classify points where *B. torquatus* occurred in territories (Spearman $r_s = 0.248$, $P = 0.083$).

3.2. Nest site selection

A. pallidiceps built nests at 1–3 m above the ground in patches of dense scrub with vines and generally without tree cover. Some nests were placed in dense bamboo thickets, where the bamboo substituted the vines as a basement for the nest. Thus nest site selection was based on similar habitat characteristics as used for foraging. The logistic regression model indicated that greater vine and bamboo cover, and lower tree cover increase the chance of a site being used for nest location (AIC = 94.550, $n = 149$, Table 3). The model accurately classified 88.6% of sites and yielded good predictive performance after internal validation (Nagelkerke- $R^2 = 0.238$, $AUC_{bootstrapped} = 0.817$).

3.3. Interspecific comparison

B. torquatus held territories that overlapped with 16 of the 26 territories of *A. pallidiceps* (61.5%), and only one minor instance of interspecific aggression was noted during the study period. However, microhabitat use of the two species, as measured by point samples, differed significantly. *B. torquatus* occurred in denser (>90% bush cover) and taller (>7.5 m) vegetation with more trees (>25% cover) than *A. pallidiceps* (Table 1). The latter was more often observed around the edges of scrub (grass cover >30%), while *B. torquatus* occurred mostly in the interior of large patches of scrub (Table 1). The logistic regression model applied to separate the habitat points used by both species included the variables bamboo, tree, grass and herb cover, vegetation density, modal height and position (AIC = 256.41, $n = 766$, Table 3). It achieved very high accuracy in classifying 94.0% of observations correctly, and performed very well (Nagelkerke- $R^2 = 0.675$, $AUC_{bootstrapped} = 0.953$).

The relative use of vegetation strata differed strongly between the two species (Fig. 1). *B. torquatus* foraged mostly on or near the ground (0–80 cm), while only 10% of *A. pallidiceps* records were at this level ($\chi^2 = 78.41$,

$df = 3$, $P < 0.001$). The latter had a mean foraging height of ca. 2 m (Table 1), both where it occurred on its own and when the two species occurred together ($\chi^2 = 5.17$, $df = 3$, $P = 0.160$).

4. Discussion

4.1. Habitat selection of the pale-headed brush-finch

The pale-headed brush-finch is described as occupying dense arid scrub and stands of *Acacia*-trees, often in ravines close to irrigation channels or natural water courses (Paynter, 1972; Ridgely and Greenfield, 2001). The most preferred habitat at the landscape scale is a heterogeneous semi-open scrubland, where small patches of low and dense scrub are interspersed with grassy clearings or herb-fields. Dense continuous scrub adjacent to open areas is similarly preferred. The nature of the scrub, whether deciduous or bamboo, appeared to be of little importance, because territories were established that contained only one type of scrub. Because of the preference for medium vegetation heights, forests and other tall scrub habitats are avoided by the pale-headed brush-finch.

Territory boundaries do not appear to be stable throughout the breeding season (Oppel, 2002), hence estimates of habitat availability based on territory boundaries might lead to bias in the calculated model (Arthur et al., 1996; McClean et al., 1998). Nonetheless we demonstrated that grassy patches are not used directly, despite being present in most territories. A potential explanation for the inclusion of open patches in territories might be food provisioning. Availability and accessibility of food resources have been demonstrated to be the main factors governing habitat use by insectivorous species (Holmes and Robinson, 1981; Keane and Morrison, 1999; Illera, 2001). Lepidopteran larvae formed a large part of the diet during the study period (Oppel, 2002). By contrast, Paynter (1972) found mostly grass seeds in stomachs of individuals collected during the non-breeding season. The pale-headed brush-finch remains in its territory throughout the year (Krabbe, pers. comm.), and both scrub and open patches might therefore be required in territories as they provide different food resources at different times of the year.

Generally, nest sites are selected to minimize detection and predation risk (Martin and Roper, 1988; Martin, 1995; Martin et al., 2000; van den Berg et al., 2001). The nests of the pale-headed brush-finch are placed on overhanging branches, vines, and bamboo stalks, and this has been suggested to preclude small mammalian predators from reaching the nest (Oppel, 2002). The presence of bamboo or other vine tangles can therefore be assumed to form the basis for nest site

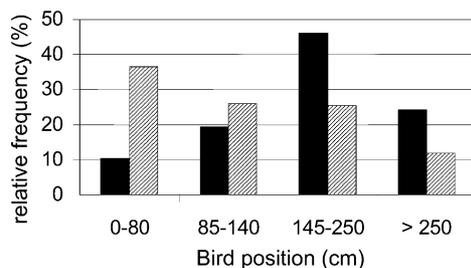


Fig. 1. Relative use of different vegetation strata for foraging and nesting by *A. pallidiceps* (black, $n = 746$) and *B. torquatus* (barred, $n = 181$) in Yunguilla Valley, Ecuador.

selection and might be a crucial factor in determining the local distribution of the pale-headed brush-finch.

4.2. Habitat selection of the stripe-headed brush-finch

The stripe-headed brush-finch prefers dense thickets under tall vegetation or forest, and avoids areas with high cover of ground vegetation (Paynter, 1978; Remsen and Graves, 1995b; Ridgely and Greenfield, 2001). Dense ground cover might inhibit ground-foraging, which is the preferred foraging strategy of the species. We could not reveal habitat selection patterns at the territory scale, which might indicate that the stripe-headed brush-finch chooses homogenous woodland territories at the landscape scale, and therefore the area included in territories is almost entirely suitable. Alternatively, small-scale differences within the homogeneous vegetation structure of occupied habitats might not have been detected with the survey methods applied. Floristic aspects were not included in our analysis, but selection for the presence of certain plant species within structurally uniform habitat patches has been described for a variety of bird species (Wiens and Rotenberry, 1981; Rotenberry, 1985).

4.3. Interspecific habitat relationships

Interspecific competition and territoriality is a result of similar habitat preferences of coexisting bird species (Orians and Willson, 1964; Cody, 1978; Rice, 1978; Sæther, 1983). Similarities in microhabitat use infer fitness costs; hence, natural selection should work towards a divergence of habitat preferences between species (Martin, 1996, 1998). Andean brush-finches are assumed to differ in microhabitat use at localities where species coexist (Remsen and Graves, 1995a).

At the study area in Yunguilla Valley, even though the stripe-headed brush-finch prefers on average taller and denser vegetation types, the territories of both species overlap widely. Interspecific territoriality and competitive exclusion resulting in non-overlapping territories, as described for other bird species (Orians and Willson, 1964; Cody, 1978; Elle, 2002), were thus not confirmed. On the other hand, the birds use different vegetation strata for foraging and the vertical segregation does not appear to result from competitive pressure. This should enable sufficient resource partitioning at sites of syntopy, and we therefore conclude that the presence of the stripe-headed brush-finch has no adverse effects on the remaining population of the pale-headed brush-finch.

4.4. 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. In the study area, succession is considered to lead to a more forest-like habitat, which is avoided by the pale-headed brush-finch. The preservation of optimal semi-open habitat would therefore require management to halt succession at an intermediate stage. Low-intensity livestock grazing has been suggested for similar purposes (Bullock and Pakeman, 1997; Redecker et al., 2002), and this does occur outside the reserve. Given the socio-economic pressures of rural Ecuador, complete exclusion of farming practices are not feasible. It would thus be desirable to come to an agreement with local farmers who hold potential brush-finch habitat, to ensure that (1) scrubland is not converted into arable fields by the burning of vegetation, and (2) grazing pressure is maintained at a low to intermediate level to preserve dense thickets. The latter could be achieved by a rotational system, where parts of a suitable brush-finch area are grazed alternately within or between years. Scrub-browsing cattle and removal of woody vegetation would be required to prevent encroachment of trees.

The invasion of bracken fern (*Pteridium aquilinum*) prevents natural succession, and is also a problem to many farmers, because it renders grassland ineffective for grazing (Paulsch et al., 2001). Fallow areas, which have been abandoned following the invasion of ferns, are of no use to farmers or brush-finches. They should therefore be afforested with scrub species to convert them to suitable habitat.

The apparent absence of birds from small isolated patches of suitable habitat (Oppel, 2002; Krabbe, pers. comm.) indicates that a conservation plan for this species should focus on large patches with appropriate landscape and microhabitat features, in order to minimize the chances of extinction from stochastic events (Simberloff, 1994; Gates and Donald, 2000; Araújo et al., 2002). These patches should be connected to facilitate genetic exchange and provide refuges for sporadically occurring climatic events (Winker et al., 1997). The dispersal and subsequent re-colonization of suitable habitat patches by the pale-headed brush-finch today is probably limited by the currently highly fragmented and largely open landscape in the upper Río Jubones valley (Gibbs, 1998; Fahrig, 2001; Lang et al., 2002; Cale, 2003). The dispersal abilities of this species need to be investigated further, and constraints need to be identified, in order to develop a management plan that considers a network of potential habitats that are within the species' current dispersal limits.

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References

- Agreda, A., Krabbe, N., Rodriguez, O., 1999. Pale-headed Brushfinch *Atlapetes pallidiceps* is not extinct. *Cotinga* 11, 50–54.
- Araújo, M.B., Williams, P.H., Fuller, R.J., 2002. Dynamics of extinction and the selection of nature reserves. *Proceedings of the Royal Society of London B* 269, 1971–1980.
- Arthur, S.M., Manly, B.F.J., McDonald, L.L., Garner, G.W., 1996. Assessing habitat selection when availability changes. *Ecology* 77, 215–227.
- Austin, G.E., Thomas, C.J., Houston, D.C., Thompson, D.B.A., 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.
- BirdLife International, 2000. Threatened birds of the world. Lynx Ediciones and BirdLife International, Barcelona and Cambridge.
- Bossuyt, B., Dercon, G., Bièvre, B.D., Cisneros, F., Deckers, J., 1997. Agro-ecological zoning of the Austro Ecuatoriano. *The Land* 1, 159–170.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. *Ecological Modelling* 157, 281–300.
- Bradley, D.W., 1985. The Effects of Visibility Bias on Time-budget Estimates of Niche Breadth and Overlap. *Auk* 102, 493–499.
- Buckland, S.T., Burnham, K.P., Augustin, N.H., 1997. Model selection: an integral part of inference. *Biometrics* 53, 603–618.
- Bullock, J.M., Pakeman, R.J., 1997. Grazing of lowland heath in England: management methods and their effects on heathland vegetation. *Biological Conservation* 79, 1–13.
- Burnham, K.P., Anderson, D.R., 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. In: McCullough, D.R., Barrett, R.H. (Eds.), *Wildlife 2001*. Elsevier Applied Science, London, pp. 16–30.
- Cale, P.G., 2003. The influence of social behaviour, dispersal and landscape fragmentation on population structure in a sedentary bird. *Biological Conservation* 109, 237–248.
- 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., Gonzaga, L.P., Krabbe, N., Nieto, A.M., Naranjo, L.G., Parker, T.A., Wege, D.C., 1992. Threatened Birds of the Americas. International Council for Bird Preservation, Cambridge.
- Dercon, G., Bossuyt, B., Bièvre, B.D., Cisneros, F., Deckers, J., 1998. Zonificación agroecológica del Austro Ecuatoriano. Promas, Universidad de Cuenca, Cuenca Ecuador.
- Elle, O., 2002. Mikrohabitatwahl und Dispersion als Hinweise auf interspezifische Konkurrenz von Mönchsrasmücke *Sylvia atricapilla* und Gartengrasmücke *S. borin* in einem Wald-Wiesen-Ökoton. *Vogelwelt* 123, 9–16.
- Fahrig, L., 2001. How much habitat is enough? *Biological Conservation* 100, 65–74.
- Fielding, A.H., Haworth, P.F., 1995. Testing the generality of bird-habitat models. *Conservation Biology* 9, 1466–1481.
- Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24, 38–49.
- Fjeldså, J., Krabbe, N., 1990. Birds of the High Andes. Zoological Museum, University of Copenhagen, Copenhagen.
- Gates, S., Donald, P.F., 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.
- Haffer, J., 1967. Interspecific competition as a possible factor in limiting the range of some trans-andean forest birds. *Hornero* 10, 438–440.
- Hanley, J.A., McNeil, B.J., 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology* 143, 29–36.
- Holmes, R.T., Robinson, S.K., 1981. Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. *Oecologia* 48, 31–35.
- Hosmer, D.W., Lemeshow, S., 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.
- Jones, J., 2001. Habitat selection in avian ecology: a critical review. *Auk* 118, 557–562.
- Keane, J.J., Morrison, M.L., 1999. Temporal variation in resource use by Black-throated Gray Warblers. *Condor* 101, 67–75.
- Lang, J.D., Powell, L.A., Kremetz, D.G., Conroy, M.J., 2002. Wood Thrush movements and habitat use: effects of forest management for Red-cockaded Woodpeckers. *Auk* 119, 109–124.
- 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., Dodd, P.W.D., Fentress, J.C., 1985. The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. *Zeitschrift für Tierpsychologie* 68, 201–214.
- Martin, T.E., Roper, J.J., 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. *Condor* 90, 51–57.
- Martin, T.E., Geupel, G.R., 1993. Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* 64, 507–519.
- 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., Scott, J., Menge, C., 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society of London B* 267, 2287–2293.
- McClean, S.A., Rumble, M.A., King, R.M., Baker, W.L., 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.
- Nagelkerke, N.J.D., 1991. A note on general definition of the coefficient of determination. *Biometrika* 78, 691–692.
- Oppel, S., 2002. The role of breeding biology, habitat selection, and cowbird parasitism for the conservation of the Pale-headed Brush-Finch *Atlapetes pallidiceps* in southern Ecuador. Unpublished M.Sc. thesis, Carl-von-Ossietzky Universität, Oldenburg, Germany.

- Orians, G.H., Willson, M.F., 1964. Interspecific Territories of Birds. *Ecology* 45, 736–745.
- Orians, G.H., Wittenberger, J.F., 1991. Spatial and temporal scales in habitat selection. *American Naturalist* 137, S29–S49.
- Paulsch, A., Schneider, R., Hartig, K., 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.
- Redecker, B., Härdtle, W., Finck, P., Riecken, U., Schröder, E. (Eds.), 2002. *Pasture Landscape and Nature Conservation*. Springer, Berlin.
- Reineking, B., Schröder, B., in press. Computer-intensive methods in the analysis of species-habitat relationships. In: *Proceedings “Genes, Bits and Ecosystems” Theory in Ecology*. Peter Lang, Frankfurt.
- Remsen, J.V., Graves, W.S., 1995a. Distribution patterns and zoogeography of *Atlapetes* brush-finches (Emberizinae) of the Andes. *Auk* 112, 210–224.
- Remsen, J.V., Graves, W.S., 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., Greenfield, P.J., 2001. *The Birds of Ecuador – Field Guide*. Cornell University Press, New York.
- Rotenberry, J.T., 1985. The role of habitat in avian community composition: physiology or floristics? *Oecologia* 67, 213–217.
- Sæther, 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.
- Schröder, B., (2000) *Zwischen Naturschutz und Theoretischer Ökologie: Modelle zur Habitateignung und räumlichen Populationsdynamik für Heuschrecken im Niedermoor*. PhD Thesis, Technical University of Braunschweig (with Software for ROC-AUC calculation and classification).
- Simberloff, D., 1994. Die Konzeption von Naturreservaten. In: Usher, M.B., Erz, W. (Eds.), *Erfassen und Bewerten im Naturschutz*. Quelle und Meyer, Heidelberg, pp. 274–291.
- Terborgh, J., Weske, J.S., 1975. The role of competition in the distribution of Andean birds. *Ecology* 56, 562–576.
- van den Berg, L.J.L., Bullock, J.M., Clarke, R.T., Langston, R.H.W., Rose, R.J., 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., Litvaitis, J.A., 1989. Resampling methods for evaluating classification accuracy of wildlife habitat models. *Environmental Management* 13, 783–787.
- Wiens, J.A., Rotenberry, J.T., 1981. Habitat associations and community structure of birds in shrubsteppe environments. *Ecological Monographs* 51, 21–41.
- Winker, K., Escalante, P., Rappole, J.H., Ramos, M.A., Oehlenschläger, R.J., Warner, D.W., 1997. Periodic migration and lowland forest refugia in a “sedentary” Neotropical bird, Wetmore’s Bush Tanager. *Conservation Biology* 11, 692–697.
- Zweig, M.H., Campbell, G., 1993. Receiver-operating characteristic (ROC) plots: a fundamental evaluation tool in clinical medicine. *Clinical Chemistry* 39, 561–577.