

Habitat selection, home range and population size of Baillon's Crake *Zapornia pusilla* in the Senegal Delta, north-west Senegal

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Summary

Knowledge of a species' ecological requirements is a prerequisite for effective conservation, particularly if the species is assumed to be declining due to modification of its primary habitats. Information about habitat suitability allows both the inference of specific habitat management measures as well as population size estimates which can facilitate the setting up of conservation priorities. As one of the least known Palaearctic breeding birds, the current knowledge of Baillon's Crake *Zapornia pusilla* comprises only very general information about the species' ecological requirements, habitat selection, extent and dynamics of home ranges or population densities within its Palaearctic-Afrotropical range. We used a multi-scale approach to assess the species' habitat requirements in the Senegal River Delta, north-west Senegal. At the individual level, we calculated Manly selection indices for 17 radio-tracked Baillon's Crakes, allowing for different levels of resource availability. Considering the entire Djoudj area including the Parc National des Oiseaux du Djoudj (PNOD), we modelled presence probability as well as population density of Baillon's Crakes based on high-resolution satellite images and capture data from field surveys in 2009–2013. Using 95% kernels, home range size was on average 1.77 ± 0.86 ha with significant differences between habitats. Both at the individual as well as population level, Baillon's Crakes preferred edge structures, selecting for trampling paths and edges along open water bodies as well as boundaries of specific vegetation stands while species composition was of less importance. Based on the regression models, we identified 9,516 ha of suitable habitat within the Djoudj area and a potential population size of 10,714 individuals (range 3,146–17,408). Although global population estimates are highly tentative, we assume the Senegal River Delta and the PNOD of outstanding significance for African and possibly also European populations of Baillon's Crake.

Resumé

La connaissance des exigences écologiques d'une espèce est une condition préalable pour la conservation efficace, en particulier si l'espèce est supposée d'être en déclin en raison de la modification de ses habitats primaires. Informations sur la favorabilité de l'habitat permettent à la fois la dérivation des mesures de gestion spécifiques, ainsi que des estimations de taille de la population qui peut faciliter l'élaboration des priorités de conservation. La Marouette de Baillon *Zapornia pusilla* est un d'espèces des moins connues parmi les oiseaux nicheurs Paléarctique. Les connaissances actuelles sur les exigences écologiques de l'espèce, la sélection de l'habitat, l'étendue et la dynamique des domaines vitaux ou les densités de population au sein de son aire de répartition Paléarctique-Afrotropical ne comprend que des renseignements très généraux. Nous avons utilisé une approche multi-échelle pour évaluer les exigences en matière d'habitat de l'espèce dans le delta du fleuve Sénégal, au nord-ouest du Sénégal. Sur le niveau de l'individu, nous avons calculé les indices de sélection Manly, en compte tenu des différents niveaux de la disponibilité des ressources

pour 17 Marouettes de Baillon observés en utilisant la télémétrie. Considérant l'ensemble de la zone Djoudj y compris le Parc National des Oiseaux du Djoudj (PNOD), nous avons modélisé à partir d'images satellitaires à haute résolution et des données de capture provenant d'enquêtes sur le terrain en 2009-2013 la probabilité de la présence ainsi que la densité de la population de la Marouette de Baillon. En utilisant l'estimation par noyau (95 %), la taille du domaine vital de l'espèce mesure en moyenne $1,77 \pm 0,86$ ha, avec des différences significatives entre des différents habitats. Tant sur le niveau de l'individu ainsi que celui de la population, la Marouette de Baillon préfère au sein de ses habitats les structures de bord, comme les pistes battues, les bords le long des plans d'eau ouverts, ainsi que les limites d'une végétation spécifique, par contre à la composition des espèces qui est d'une moindre importance. Basé sur les modèles de régression, nous avons identifié 9,516 ha d'habitat favorable dans la zone Djoudj et une taille de population potentielle de 10714 individus (étendue 3.146 à 17.408). Bien que les estimations de la population mondiale soient très provisoires, nous supposons que les zones humides du delta du fleuve Sénégal et le PNOD ont une importance exceptionnelle comme habitat pour les populations africaines et peut-être aussi européennes de la Marouette de Baillon.

Introduction

Habitat selection is influenced by a number of proximate and ultimate factors (Block and Brennan 1993), including habitat structures, floristics, competition, food availability and predation risk (MacArthur and MacArthur 1961, Southwood 1977, Noon 1981, Muller *et al.* 1997). The prevalent definition of habitat selection is the disproportionate use of environmental conditions to influence survival and ultimate fitness (Block and Brennan 1993), which takes place at multiple spatial and temporal scales (Johnson 1980, Kotliar and Wiens 1990). Landscape-scale features (macrohabitat) are correlated with the distribution and abundance of populations and often describe discrete arrays of, e.g., specific vegetation types. Particular features of an environment that act as proximal cues to stimulate settling of an individual animal constitute its microhabitat which can represent specific habitat patches or individual home ranges (Block and Brennan 1993). When investigating habitat selection, it is widely recommended to include more than one spatial scale, preferably within a nested hierarchy (Wiens *et al.* 1987, Kotliar and Wiens 1990) as it can be difficult or impossible to determine in advance the most ecologically relevant scale for different environmental variables.

The current knowledge of Baillon's Crake *Zapornia pusilla* ecology is very limited, comprising only general information about the species' ecological requirements and habitat selection. Few specific studies exist, which are all descriptive in nature (Noll 1924, Szabó 1970) and compendia mostly report anecdotal observations or refer to other Palearctic *Porzana* and *Zapornia* species (e.g. Glutz von Blotzheim *et al.* 1994). Typical habitats include palustrine wetlands, freshwater to saline, with dense vegetation such as marshes, floodplains, inundated grasslands and irrigated crops (Taylor and Van Perlo 1998). Suitable wetlands are often seasonally and only shallowly flooded with water levels ranging from a few to 30 cm (Glutz von Blotzheim *et al.* 1994, Taylor and Van Perlo 1998). However, outside the breeding season the species is reported to occur in a wider variety of habitats with water levels up to 2 m (Marchant and Higgins 1993). Vegetation cover is typically dominated by relatively fine-stemmed sedge and grass species, including the genera *Carex*, *Cyperus*, *Eleocharis*, *Juncus*, *Scirpus* and *Phalaris* (Szabó 1970, Glutz von Blotzheim *et al.* 1994, Taylor and Van Perlo 1998) which form a dense and usually uniform vegetation cover. Nesting locations are often associated with tussocks of e.g. *Eleocharis* spp. or tall forbs such as *Althaea officinalis* (Szabó 1970) and nests consist predominantly of fresh and soft plant material (Glutz *et al.* 1994). Glutz *et al.* (1994) described the habitats occasionally comprising ditches and sparsely vegetated shallows and Taylor and Van Perlo (1998) reported that the species normally forages in unvegetated spots. But the significance of edge structures, open water bodies and other small-scale features for Baillon's Crake habitat has not been investigated yet.

Likewise, virtually nothing is known about the extent and dynamics of the species' home ranges or population densities. Taylor (1997) provided the only estimate for breeding Baillon's Crakes for a wetland in KwaZulu-Natal, South Africa, while densities in European breeding grounds are assumed to be generally marginal (e.g. Dies and Dies 2003) owing to the small European population which comprises only 740–3,200 breeding pairs (BirdLife International 2004).

Across both its European and African ranges, the species is considered to be declining as a consequence of severe habitat degradation, e.g. the cultivation and drainage of ephemeral wetlands (Koshelev 1994, Taylor and Van Perlo 1998). Accordingly, only a handful of observations are reported annually both for its Palaearctic and Afrotropical breeding grounds (e.g. DAK 2010). All the more remarkable was the discovery of a potentially large breeding population of Baillon's Crake in the Senegal River Delta, north-west Senegal (Seifert *et al.* 2012), where the species was only assumed to spend the non-breeding season (Roux and Morel 1966). Based on capture data from 2007, Flade (2008) presumed the floodplains of the Parc National des Oiseaux du Djoudj (PNOD) to accommodate the majority if not the entire European population during the Northern hemisphere winter months. By now, the area's significance exclusively as a non-breeding site for European migrants is questionable after the observation of many individuals reproducing both in the PNOD and Diawling National Park (Mauritania) at that time (Seifert *et al.* 2012, 2016, Seifert & Sidaty 2013). However, local Baillon's Crake abundance may surpass by far any other number estimated for known populations, which would underline the relevance of the PNOD and adjacent floodplains throughout the Senegal River Delta as important refuge.

Knowledge of a species' ecological requirements is a prerequisite for effective conservation (e.g. Luck 2002), particularly if the species is assumed to be declining due to modification and degradation of its habitats. Information about habitat suitability allows both the inference of specific habitat management measures as well as models to estimate potential distribution or population sizes (Guisan and Zimmermann 2000) which can facilitate the set-up of conservation priorities. Accordingly, the aim of this study was to (1) determine factors that influence occurrence of Baillon's Crakes both on a macro- as well as microhabitat scale. Thereby we address the question whether structural characteristics of vegetation or plant species composition are more relevant for the species' habitat selection. Furthermore, we intend to (2) predict the extent of suitable habitat and (3) estimate the potential maximum population size of Baillon's Crakes within and in the vicinity of the PNOD in order to assess the significance of the Senegal River Delta for the species.

Material and methods

Study area

Our fieldwork was performed within and north of the PNOD (16°20'N, 16°12'W), the so-called Djoudj area (Figure 1). The study area (in total 41,184 ha) comprises a network of former tributaries of the Senegal River, seasonal lakes and shallowly inundated floodplains which are nowadays artificially flooded during the rainy season between July and October (Fall *et al.* 2003). In the course of the subsequent dry season, the majority of the area, vast grass and sedge marshes, falls dry successively. The typical vegetation consists of ephemeral salt-resistant plant species such as *Eleocharis mutata*, *Oryza longistaminata*, *Scirpus maritimus*, *S. littoralis* and *Sporobolus robustus*. Cattail stands *Typha australis* prevail at locations with stronger influence of freshwater and along the banks of the Senegal River.

Study sites and capture of Baillon's Crakes

Baillon's Crakes were caught in 23 geographically separated study sites between December and March during our field work periods in the dry seasons 2009 ($n = 10$), 2009/2010 ($n = 9$) and 2013

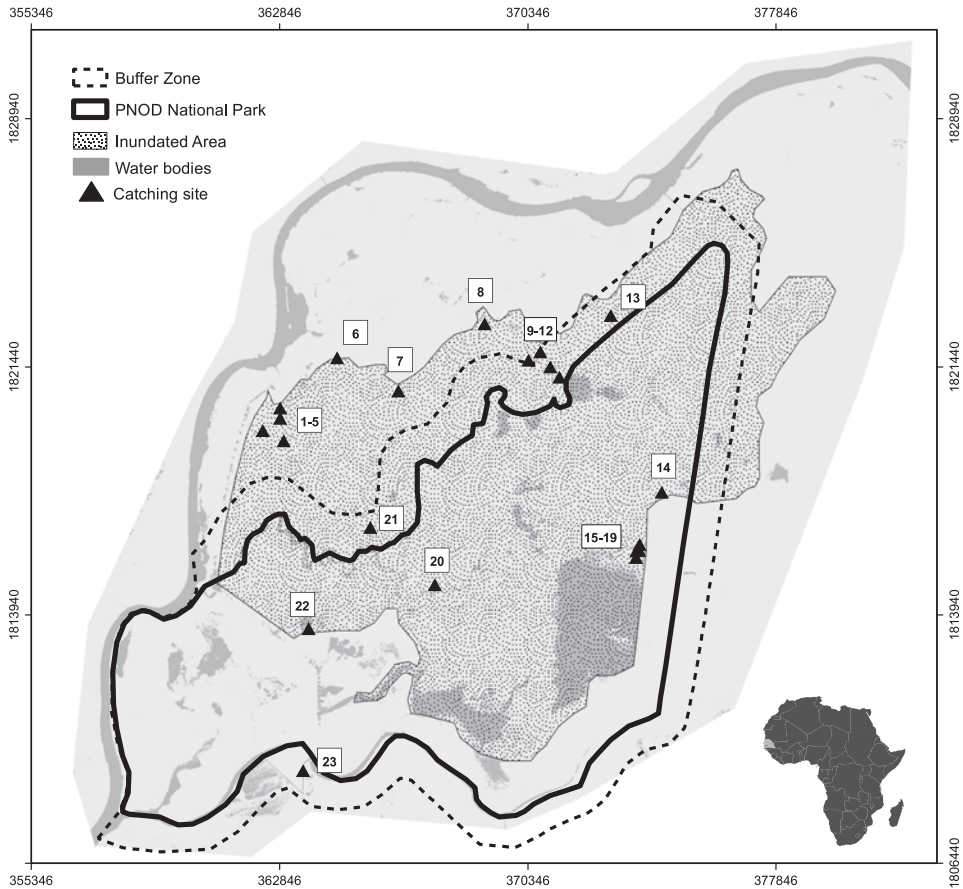


Figure 1. Study area (Djoudj) and location of 23 study sites (1 -5 = Tiguet I - V, 6 = Tiguet East, 7 = Debi West, 8 = Debi East, 9-12 = Crocodil I - IV, 13 = Diadiah, 14 = Grand Lac North, 15-19 = Grand Lac I - V, 20 = Gainthe, 21 = Tiguel, 22 = Lac Tantale, 23 = Typha).

($n = 4$) (Figure 1). The capture sites were selected by sampling different vegetation types all over the study area which a) provided enough vegetation cover and b) were sufficiently inundated with water levels varying from five to 40 cm. Based on literature on habitat requirements (e.g. Szabó 1970, Taylor and Van Perlo 1998) these settings were regarded as minimum preconditions for the potential presence of Baillon's Crakes. Birds were caught with a set of 30 - 40 cage traps (Bub 1995) which were installed at regular intervals of approximately 10 m along transect lines within the study sites. Captured birds were aged into adult, juvenile and chick, and body measurements as well as respective trap coordinates were recorded.

Telemetry

In total, 23 adult birds with body mass >40 g were equipped with 1.3 g lightweight radio-transmitters (PIP3 single celled tags, Biotrack Ltd.) in the field seasons 2009 ($n = 7$) and 2009/2010 ($n = 15$) at the three study sites Grand Lac (GL), Tiguet (TG) and Debi (DB, only one individual in 2009). Transmitters were attached using a leg-loop harness following Haramis and Kearns (2000). Radio-tracking was conducted with a hand-held three-element Yagi-antenna connected to a Sika receiver

(Biotrack Ltd.). Tagged individuals were recorded starting 48 h after capture. Locations of individuals were collected every second (2010) or third day (2009) from 07h00 to 14h00 and occasionally in the afternoons from 16h00 to 19h00. Thereby we tried to obtain relocations for each individual at least three times in the course of the day with approx. 1.5 h between the fixes. Relocations were assessed by triangulation (White and Garrot 1990) using three to five bearings, and LOCATE (Nams 2006) was used to determine Baillon's Crake locations. All directions were recorded within five minutes to minimise errors due to the birds' movements. Radio-tracking was performed only by N. Seifert in both field seasons.

Estimation of home ranges

Only individuals with >10 relocations and a tracking period of > five days were included in the home range estimation. As we detected large movements after capturing the birds, we did not consider the location of the respective cage traps in the analyses. Home range boundaries were calculated with a fixed kernel estimator (Hooge and Eichenlaub 1997) reporting the 95% kernel density home range for each Baillon's Crake using the R-package "adehabitatHR" (Calenge 2006). The smoothing parameter h was estimated via the reference bandwidth "href" as the number of relocations was too small for some individuals (<20) to apply a least squares cross-validation procedure (e.g. Seaman and Powell 1996). In order to detect directional shifts in the position of the home ranges, we calculated the centroid for each daily set of relocations per bird and measured the distances and directions between the first and last centroid.

Environmental variables

Land cover classes in GL and TG

As nearly all radio-tracked Baillon's Crakes were followed in the two study sites Grand Lac (GL) and Tiguet (TG), we aimed at generating high resolution vegetation maps for each site to capture small-scale features which might be ecologically relevant for Baillon's Crake habitat selection. For this purpose, we took aerial photographs during the field season 2009/2010 using a Sutton Flow kite (Kite Aerial Photography) which was flown over the sites following transects in N-S (TG) or E-W (GL) direction. A 7-megapixel point & shoot camera (Canon Powershot G6) combined with a 2 GB storage medium was mounted on a Picavet-suspension approx. 50 m underneath the kite. Imagery was obtained in 3072 x 2304 pixel images taken at a shooting frequency of one image per minute. The ground resolution of these images depends on the flying height of the kite (e.g. 5 cm at a flying height of 130 m above the ground, Becker *et al.* 2008). For ground verification, we installed a 30 x 30 m grid of white paper plates with known GPS position (4 m accuracy) as ground control points within the sites. These points were later used to georectify and merge the pictures into one image per site using ArcGIS 10.1 (ESRI 2015). Each site was photographed twice to ensure sufficient overlap of images.

The georectified imagery was polygonised and classified by hand, using ArcGIS, defining six classes of herbaceous vegetation types dominated by one plant species, nine classes of mixed stands, three classes of tree/shrub species as well as other land cover classes such as zones with scarce vegetation cover (<50%), unvegetated soil, open water and trampling path (Table 1, Appendix S2, S3 in the online supplementary material). Two raster maps were obtained with a resolution of 0.25 m² per pixel cell by rasterizing the resulting land cover maps.

Land cover classes Djoudj area

Land cover data for the entire study area was obtained from the classification of high resolution satellite images taken in January 2011 with a resolution of 0.5 m² (Tegetmeyer *et al.* 2014). The derived order synonym vegetation and land cover map with a resolution of 1 m² per pixel cell

Table 1. Land cover classes of vegetation maps and additional structural habitat parameters for the entire Djoudj area (DJOUJ) and study sites Grand Lac (GL) and Tiguet (TG). Fraction of land cover classes given in % of total area.

* % of 130 x 130 m pixel cells containing edge structures of respective vegetation class.

Variable	Description	DJOUJ	GL	TG
ELE	<i>Eleocharis mutata</i>	5.05	1.00	2.70
ORYZA	<i>Oryza longistaminata</i>	2.13		36.46
SCL	<i>Scirpus littoralis</i>	15.01	57.49	
SCM	<i>Scirpus maritimus</i>	8.89		17.22
SPORO	<i>Sporobolus robustus</i>	3.83	13.92	4.77
TYPHA	<i>Typha australis</i>	13.65	1.41	0.05
ELE_ORY	Mixed stands <i>E. mutata</i> , <i>O. longistaminata</i>			0.89
SCM_ELE	Mixed stands <i>S. maritimus</i> , <i>E. mutata</i>			13.45
SCM_ORY	Mixed stands <i>S. maritimus</i> , <i>O. longistaminata</i>			5.84
SPORO_ELE	Mixed stands <i>S. robustus</i> , <i>E. mutata</i>			0.80
SPORO_SCL	Mixed stands <i>S. robustus</i> , <i>S. littoralis</i>		7.12	
SPORO_SCM	Mixed stands <i>S. robustus</i> , <i>S. maritimus</i>			4.35
SPORO_SCM_ELE	Mixed stands <i>S. robustus</i> , <i>S. maritimus</i> , <i>E. mutata</i>			1.43
TYPH_ELE	Mixed stands <i>T. australis</i> , <i>E. mutata</i>			0.06
TYPH_SCM	Mixed stands <i>T. australis</i> , <i>S. maritimus</i>			0.77
ACA	<i>Acacia</i> sp.		0.62	0.24
SALVA	<i>Salvadora persica</i>		0.08	
TAMAR	<i>Tamarix senegalensis</i>		0.91	0.02
WOOD	Woody species (<i>Acacia</i> , <i>Salvadora</i> , <i>Tamarix</i> etc.)	12.59		
RICE	Cultivated rice paddies	6.24		
Veg.50	Vegetation cover <50%. Typically scarce vegetation close to open water bodies		1.59	4.54
Water	Open water	10.34	8.00	4.25
SOIL	Open soil	13.79	2.38	
SAND	Sand	8.48	4.64	
Edge_ELE	Edge length of patches of <i>E. mutata</i>	19.84*		
Edge_ORY	Edge length of patches of <i>O. longistaminata</i>	13.54*		
Edge_SCL	Edge length of patches of <i>S. littoralis</i>	47.14*		
Edge_TYPH	Edge length of patches of <i>T. australis</i>	49.56*		
Edge_Water	Edge length of open water bodies		0.37	0.66
Edge_Path	Length of trampling pathes		0.48	1.49

contained six classes of dominant vegetation (Table 1) and five general land-cover classes: woody vegetation (e.g. *Acacia* sp., *Tamarix senegalensis*, *Salvadora persica*), sandy soil, open water, bare soil and cultivated rice paddies.

Habitat selection analyses

Habitat selection was analysed considering multiple scales, both on a population as well as an individual level following Thomas and Taylor (1993) who differentiated between three designs which correspond to different levels of selection identified by Wiens (1973). While first order selection applies to the level of population and e.g. its geographic range, second and third order selection occur at the individual level, either at the scale of local sites or plot patterns in territories (second order) or patterns of utilisation (third order).

Individual level (Design II, III)

For second and third order habitat selection, we compared the use and availability of each habitat class by calculating the Manly selection ratio w_j

$$w_j = \frac{u_j}{a_j}$$

where u_j is the proportion of use of the habitat class j and a_j is the proportion of availability of this habitat class (Manly *et al.* 2002). Habitat selection ratios were significant if their 95% confidence intervals did not include 1; values >1 indicated selection while values <1 indicated avoidance (Manly *et al.* 2002).

Firstly, habitat use was measured for each radio-tracked individual (= 95% kernel density home range), but availability was assumed to be the same for all individuals, considering the entire extent of the respective study site (= Design II). Secondly, both use and availability of the habitat classes was measured for each individual, implying that availability varies from one animal to the other (= Design III). Accordingly, for each radio-tracked Baillon's Crake, available habitat units correspond to the pixel cells of the 0.25 m² vegetation maps (GL and TG) falling inside the limits of the 95% kernels. Used habitat units correspond to the pixel cells containing the relocations. To account for the GPS accuracy of ± 4 m, we extracted all pixel cells in a radius of 4 m around each relocation. In total 16 (GL) and 18 (TG) different habitat classes as well as edge length of open water bodies and trampling paths were considered (Table 1).

Population level

For modelling habitat selection on a landscape level in order to assess the extent of suitable habitat and infer a potential population size for the Baillon's Crake in the study area, we used both logistic regression models as well as Poisson models based on capture data of the 23 study sites (Figure 1).

We subdivided the trap transects in each study site into 130 x 130 m blocs corresponding to the mean home range size of 1.77 ha (see Results) and summed up the number of Baillon's Crakes captured within the first three days after the installation of the transect. By this, we derived two response variables comprising count and presence/absence data for a total of 108 trap transect blocs, respectively.

The values of explanatory variables were obtained from a 1.77 ha circle ($r = 75.06$ m) drawn around each midpoint of the transect blocs, extracting the sum of pixel cells for each of the 11 land cover classes of the study area's vegetation map. In addition, we calculated the edge length of patches of different vegetation classes to consider effects of edge structures in our models.

The vegetation map was used to generate a 130 x 130 m raster layer for each of the vegetation and land cover classes, every pixel cell containing the sum of the underlying 1 m² pixel cells per class. The resolution of this set of raster layers corresponded to the area sampled in each trap transect bloc.

To derive the presence probability of Baillon's Crake in a given 130 x 130 raster cell, we used logistic regression models with a logit link function, assuming a Bernoulli distribution (McCullagh and Nelder 1989) for the response variable. A Poisson model was chosen to estimate population density for a given raster cell. As the 108 trap transect blocs were grouped into 23 geographically separated sites (Figure 1), we had to consider that transect blocs within one study site are more similar to each other than to blocs of other sites. Accordingly, we included "site" as a random factor, using generalised linear models (Bolker *et al.* 2009).

After controlling for collinearity, we included the following explanatory variables as main effects into our global models: ELE, ORZYA, SCL, SCM, SPORO, TYPHA, Water and WOOD as well as Edge_ELE, Edge_ORY, Edge_SCL and Edge_TYPH (Table 1). All numerical variables were centred and standardised. Model assumptions were tested by graphical analysis of residuals. We used a stepwise backward selection to choose the best model using Akaike's information criterion corrected for small sample size (AICc, Burnham and Anderson 2002; Appendix S1). To assess the predictive performance of the best models, we performed cross-validation, allocating the data into cross-validation groups corresponding to the 23 separate study sites. The models were fitted using 22 of our 23 sites and the predictive power was tested using the remaining site. The cross-validation score was calculated as the sum of the squared differences between cross-validated predictions and

our observation data. The model predictions were graphically compared with the probability of presence (logistic model) and the number of the individuals of the count data (Poisson model), respectively.

Predicting the extent of suitable habitat and population size

The best (final) models were used to predict the presence probability (logistic model) and density of Baillon's Crake (Poisson model) for each 100 x 100 raster cell. We calculated the potential population size as well as the lower and upper limit of the 95% credible interval (CI) by summing up all predicted density values. The area of potentially suitable habitat was determined by calculating the sum of all raster cells with a presence probability of >0.5. All spatial data were handled in ArcGIS 10.1 and 10.2 and the R-package "raster" (Hijmans *et al.* 2014) and "maptools" (Bivand and Lewin-Koh 2014). GLMMs were fitted using the glmer function from the "lme4" package (Bates *et al.* 2014).

Results

Home ranges

Mean home range size was 1.77 ± 0.86 ha (minimum HR: 0.48 ha, maximum HR: 3.41 ha; Table 2, Appendix S2, S3). We found no significant effect of number of fixes or tracking days on home range size (n fixes: $F_{1,16} = 2.71$, $p = 0.11$, n days: $F_{1,16} = 2.39$, $p = 0.14$). Home ranges were significantly larger in GL (Wilcoxon-test, $W = 59.5$, $P = 0.008$) with a mean of 2.42 ha

Table 2. Key data of Baillon's Crakes radio-tracked during the field seasons 2009 and 2009–2010 in three sites (DB = Debi, GL = Grand Lac, TG = Tiguet) within and in the vicinity of the PNOD, Senegal. Home range size is estimated by 95% fixed kernels.

ID	Site	Fixes	Tracked Days	Period of observation	Distance Trap-1st fix	Home range (ha)	Distance 1st and last fix	Direction (°)
150312B	DB	41	25	03.02.-27.02.2009	526	2.78	153	90
150063	GL	79	50	24.12.2009-29.01.2010	141	2.33	265	238
150152	GL	21	12	23.12.2009-10.01.2010	96	1.91	87	256
150154	GL	62	17	23.02.-11.03.2009	288	1.74	137	202
150277	GL	31	24	24.12.2009-17.01.2010	115	1.85	61	135
150294	GL	5	3	04.02.-06.02.2010	138			
150354	GL	34	11	13.01.-24.01.2009	315	3.41	331	236
150388	GL	12	7	14.01.-21.01.2010	49	3.29	139	236
150007	TG	18	7	14.01.-20.01.2010	NA	0.48	49	183
150075	TG	25	13	30.12.2009-11.01.2010	30	0.79	270	207
150088	TG	3	3	29.01.-01.02.2010	NA			
150113	TG	20	12	31.12.2009-11.01.2010	148	1.75	100	102
150180	TG	44	35	29.12.2009- 02.02.2010	67	1.74	45	152
150206	TG	12	13	16.01.-28.01.2010	269	0.85	26	308
150218	TG	4	1	28.12.2009	151			
150260	TG	21	13	17.01.-29.01.2009	133	1.76	184	187
150281	TG	12	6	21.01.-27.01.2009	101	0.58	148	181
150312	TG	13	8	22.01.-29.01.2009	190	0.85	157	171
150339	TG	25	16	19.01.-04.02.2010	194	1.79	16	310
150371	TG	12	3	23.01.-25.01.2009	377		53	83
150416	TG	26	15	20.01.-04.02.2010	6.6	2.22	38	160
150429	TG	9	5	17.01.-21.01.2010	210			
150460	TG	7	8	31.12.2009-07.01.2010	489			
$n = 23$	mean	23.30	13.35		192.08	1.77		

compared to 1.28 ha in TG. It should be noted that, generally, some individuals in GL could be tracked over long periods (Table 2) though we did not find the number of fixes or tracking days significantly different at the two study sites (Wilcoxon-test, n fixes: $W = 44.5$, $P = 0.12$; n days: $W = 39$, $P = 0.35$).

Individuals moved between initial capture and first relocation on average 192.08 ± 121.45 m (e.g. Figure 2), while later movements between consecutive daily centroids during the tracking period were shorter with a mean of 35.68 ± 12.49 m. Only for three birds detected distances between capture and first relocation corresponded to the mean daily movement (Table 2). Both in GL as well as in TG a tendency was observable that centroids of daily relocations shifted towards south (Fig. 3). Eighty percent of birds radio-tracked at GL showed a south-westerly movement, while directions in TG were less distinct with 63% southerly, but also easterly and north-westerly directions (18% each). Considering only birds for which movements were >130 m (corresponding to edge length of mean home range size), movements were consistently oriented towards south and south-west (Figures 2, 3).

Habitat selection

Individual level

Comparing the composition of land cover classes within the 17 home ranges with the study sites' overall composition (Design II), structures such as trampling paths and edges along open water bodies were used more than expected based on their availability both in GL and TG (Figures 4a,b, 5a,b). Homogeneous stands of *E. mutata* were significantly selected by birds radio-tracked in GL, while Baillon's Crakes in TG tended to prefer *O. longistaminata*. Stands of *S. littoralis* were avoided at GL despite the species' clear dominance at the study site. Whereas shrubs and trees were significantly avoided at GL, home ranges of three birds at TG comprised single acacia trees (Figure 4b). In general, the wide confidence intervals of most of the estimates yielded high individual variability in selection of the respective land cover classes.

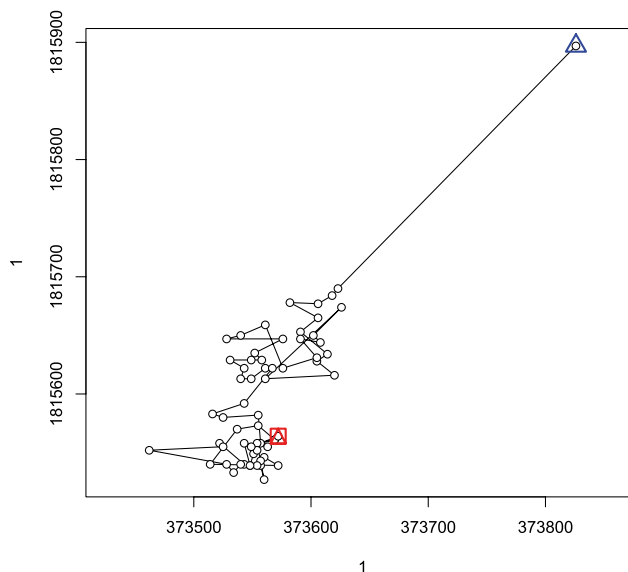


Figure 2. Individual trajectory for radio-tracked bird ID 150154. Triangle: position of the trap. Square and triangle: last relocation. Lines connect consecutive relocations.

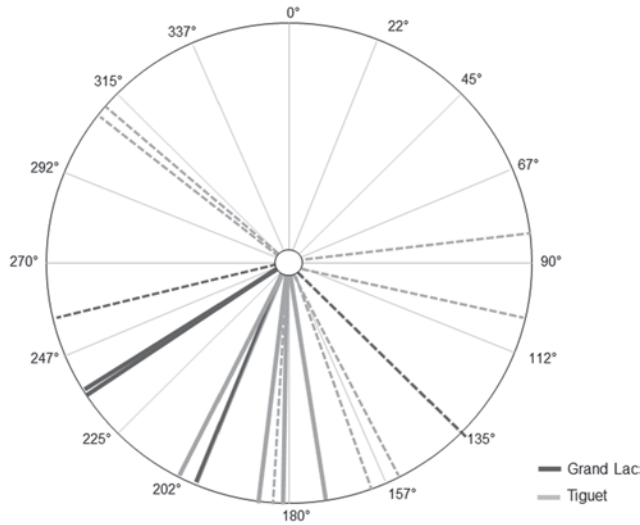


Figure 3. Directional shifts in home ranges (first and last centroid of daily relocations). Dark grey = GL, light grey = TG. Solid lines = movements >130 m, dashed lines = movements <130 m.

Considering both use and availability of habitat parameters for each radio-tracked Baillon's Crake individually (Design III) by comparing composition of land cover classes at the bird's relocations with the overall composition within its respective 95% Kernel, only the global Manly selection ratio for Edge_water proved to be significantly positive for GL (Figure 4c). Overall, selection was highly variable across the radio-tracked individuals identifying no general preference for specific habitat parameters (Figures 4d, 5d).

Population level

The best models included four (logistic model) and five (Poisson model) habitat variables, respectively (Table 3a,b, Appendix S1). Thereby, edge structure of *T. australis* and *O. longistaminata* as well as *S. littoralis* stands affected probability of presence of Baillon's Crakes positively, while it was negatively correlated to the occurrence of monotonous stands of *T. australis* (Table 3a). Density of Baillon's Crakes was positively affected by edge structures of *E. mutata* and *O. longistaminata*. However, densities decreased when area of *E. mutata*, *T. australis* and *S. maritimus* increased (Table 3b). The cross-validation scores of the best models were 0.233 and 2.595 (logistic, Poisson), respectively. Cross-validated model prediction versus presence probability (Fig. 6a) and captures (Fig. 6b) revealed that both models could be used for relatively reliable predictions of presence/densities in comparable habitats.

Habitat suitability and population size estimate

We applied the logistic model to the land-cover raster data set obtained from the satellite picture (Tegetmeyer *et al.* 2014) and derived a map of probability of presence for Baillon's Crakes in the Djoudj area (Figure 7). By using presence probability as a proxy of habitat suitability, the predicted area of potential Baillon's Crake habitat with a probability >0.5 sums up to 9,516 ha (95% CI: 3,138–19,166 ha). Applying the Poisson model to the land-cover raster data set and summing predicted numbers of individuals for each raster cell, we obtained a potential population size of 10,714 Baillon's Crakes in the study area. The 95% confidence interval ranged from 3,146 to 17,408 individuals.

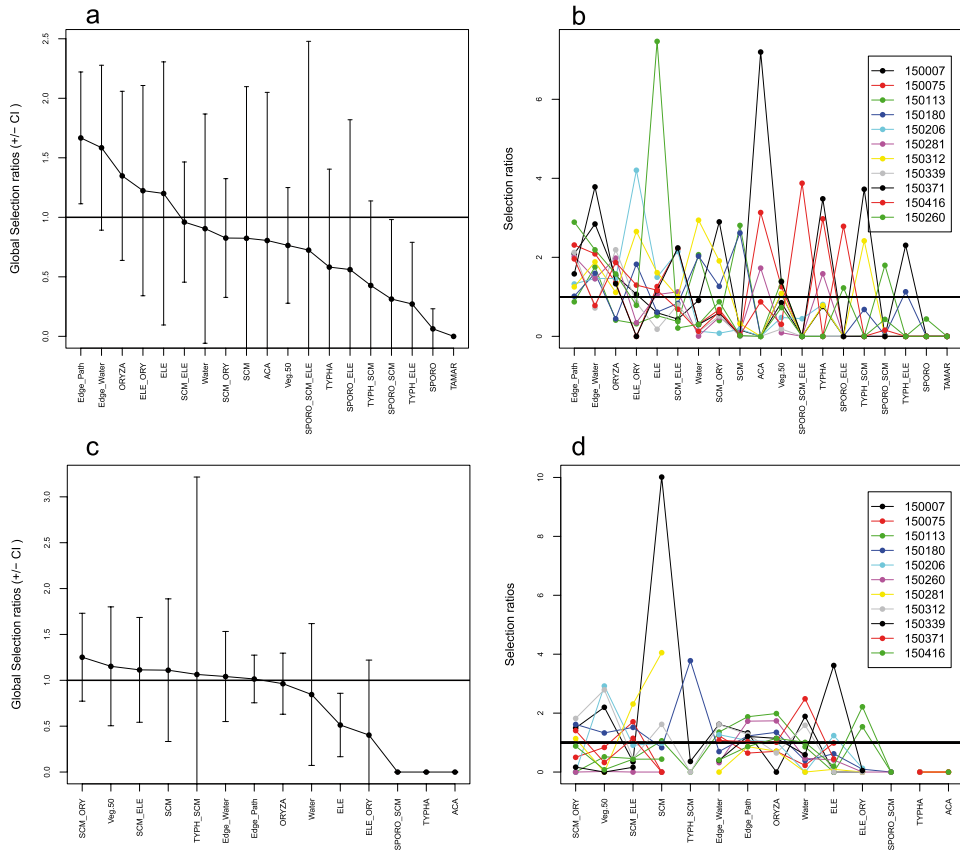


Figure 4. a & c) Global and b & d) individual Manly selection ratios (\pm SE) for Design II (a, b) and Design III (c, d) for six Baillon's Crakes radio-tracked at study site GL. Ratios are significant if their 95% confidence intervals do not include 1; values >1 indicate selection, values <1 indicate avoidance.

Discussion

Home ranges

The extent of a home range might be governed by a multitude of different factors. Differences of home range sizes can be attributed to sex (Legare and Eddleman 2001), age (Krüger et al. 2014) or body conditions (e.g. Harestad and Bunnell 1979). Home range size often negatively correlates with resource abundance (Village 1982, Glenn et al. 2004), leading to strong variation between habitat types (Conway et al. 1993, Rush et al. 2010). Furthermore, territories in the breeding season are often smaller than those established during the non-breeding season, as e.g. in the case of Clapper Rails *Rallus longirostris* which expand their home ranges from a median of 0.28 ha to several square kilometres after breeding (Eddleman and Conway 1998, Cumbee et al. 2008).

With a mean size of 1.77 ha, the home range estimates for Baillon's Crane in the Senegal River Delta are in the range of home range sizes inferred from radio-tracking reported for other small rallid species such as the Black Rail *Laterallus jamaicensis* (0.51–3.1 ha; Legare and Eddleman 2001), Yellow Rail *Coturnicops noveboracensis* (1.2 ha, Bookhout and Stenzel 1987) and Spotted Crane *Porzana porzana* (median 1.32 ha, Schäffer 1999). We found the variability in home range size to be rather low compared to other studies (e.g. Spotted Crane 0.44–55.46 ha, Schäffer 1999; King Rail *Rallus elegans* 0.8–32.8 ha, Pickens and King 2013). However, considering the short

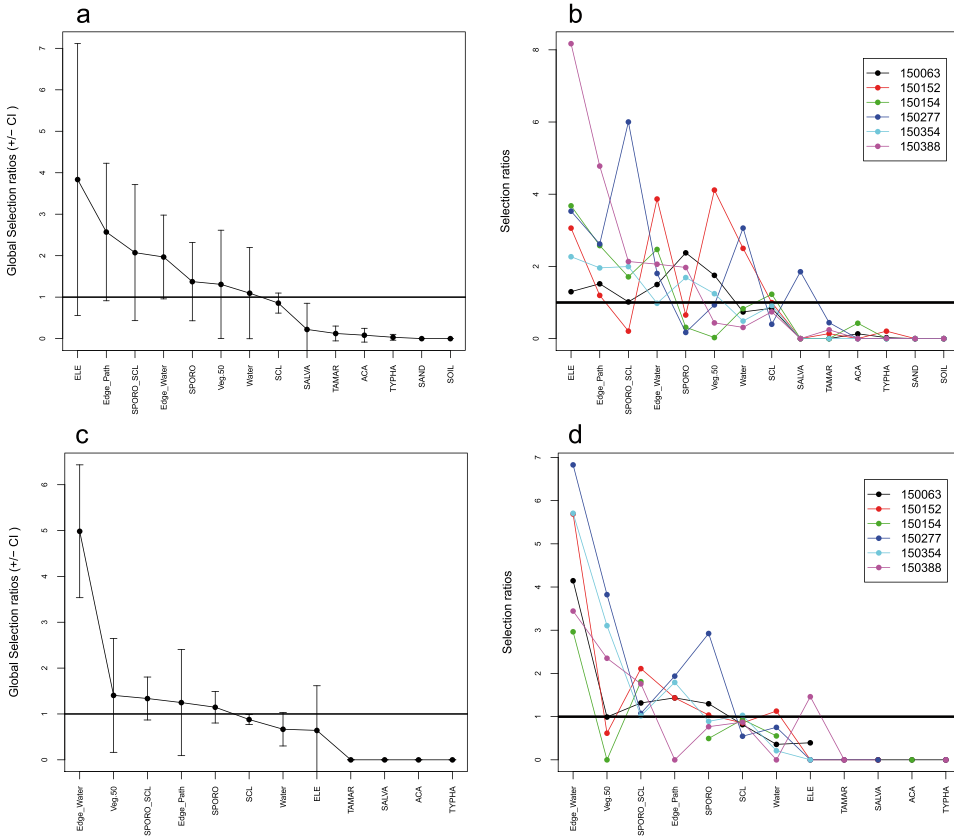


Figure 5. a & c) Global and b & d) individual Manly selection ratios (\pm SE) for Design II (a, b) and Design III (c, d) for eleven Baillon's Crakes radio-tracked at study site TG. Ratios are significant if their 95% confidence intervals do not include 1; values >1 indicate selection, values <1 indicate avoidance.

range of our transmitters of approximately 1,000 m, we might have missed longer movements of birds which would have increased home range sizes. Dispersal-like movements following the breeding season are generally poorly investigated in rallids but observed for Virginia Rail *Rallus limicola* and Sora Rail *Porzana carolina* (Johnson and Dinsmore 1985) of which some individuals were found to start moving distances >500 m when chicks became independent. We can only speculate whether the abrupt loss of signals of four birds in GL and two birds in TG despite "favourable" water levels in the field season 2009/2010 (N. Seifert unpubl. data) can be interpreted as such short-range dispersal movements. Rapidly decreasing water levels of $0.5 \text{ cm}^* \text{ day}^{-1}$ in the course of the season (Seifert *et al.* 2015) might have been a reason for birds to leave the study sites as hypothesised for four birds in TG (2009/2010) where home ranges were dry when the birds' signal was lost. Other birds shifted their home ranges towards zones which were still inundated as indicated by southward (TG) and south-westward (GL) movements which corresponded to the respective relief in GL and TG (Franke 2013, N. Seifert unpubl. data).

In general, interpretation of our data is complicated by the mostly unclear reproductive status of the radio-tracked birds. The breeding season in the Senegal River Delta starts in October and may last until January/March, depending on water levels in the PNOD and its vicinity (Seifert *et al.* 2012). Accordingly, within the period December–March, some birds might still be breeding

Table 3. Standardized effect sizes (\pm SE) of the best models (logistic, Poisson).

	Estimate	SE	z value	Pr(> z)	
a) Binomial model					
Intercept	-0.3047	0.2719	-1.121	0.262	
SCL.sc	0.4603	0.3188	1.444	0.148	
TYPHA.sc	-1.7378	0.8946	-1.942	0.052	.
EdgeORY.sc	0.7469	0.3484	2.144	0.032	*
EdgeTYPH.sc	1.1724	0.8089	1.45	0.147	
b) Poisson model					
Intercept	-0.467	0.1809	-2.582	0.009	**
ELEO.sc	-0.7758	0.2936	-2.642	0.008	**
TYPHA.sc	-0.6442	0.2428	-2.653	0.007	**
SCM.sc	-0.4453	0.1628	-2.735	0.006	**
EdgeELE.sc	0.6416	0.2381	2.695	0.007	**
EdgeORY.sc	0.4025	0.1176	3.423	0.0006	***

while others have already completed reproduction. Furthermore, some Baillon’s Crakes might as well stem from distant breeding areas and use the Senegal River Delta as a non-breeding site (Seifert et al. 2016). Accordingly, our data do not allow an explicit statement about the size of Baillon’s Crakes’ breeding home ranges but rather give an approximation possibly comprising breeding, post-breeding and potentially wintering home ranges. Certainly, longer observation periods would help e.g. to delineate possible core areas (frequently visited spots within the home range) and thus the deduction of the birds’ status.

Consistent for almost all radio-tracked individuals was the observation of longer distances between the location of capture and the first relocations after 48 h. Based on a very low recapture probability observed during our field seasons in the Senegal River Delta (total number of captured Baillon’s Crakes 2007–2013: 337 individuals, of which 15 individuals were recaptured within the same field season) and for other crane species in the Peene River valley, northeast Germany (A. Eilers, B. Herold, N. Seifert unpubl. data), we hypothesise that Baillon’s Crakes respond rather sensitively on disturbances such as capture. Besides the possibility that birds become trap-shy our data suggest that intrusions can lead to evasive movements, forcing the birds to abandon former

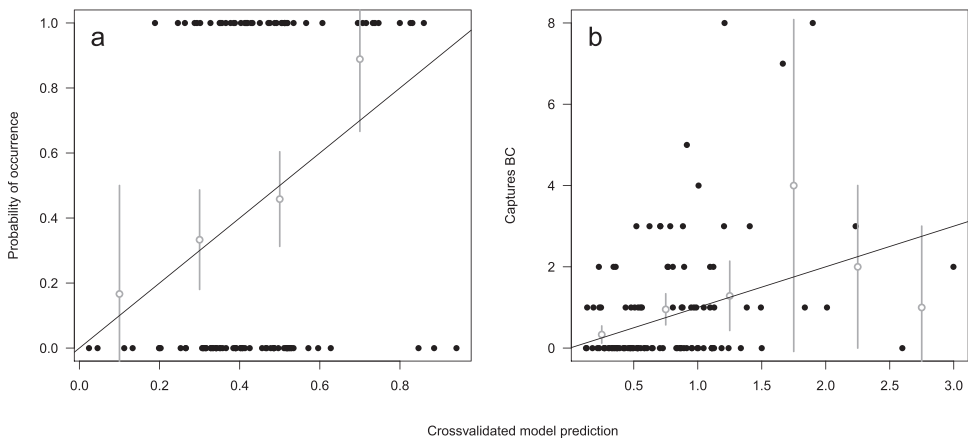


Figure 6. Cross-validated model predictions versus probability of presence (a) and captures (b). Grey dots indicate grouped mean values (and 95% credible interval). The black line indicates perfect fit. Mean values below the line indicate underestimation of presence probability/densities while values above the line show overestimation by the models.

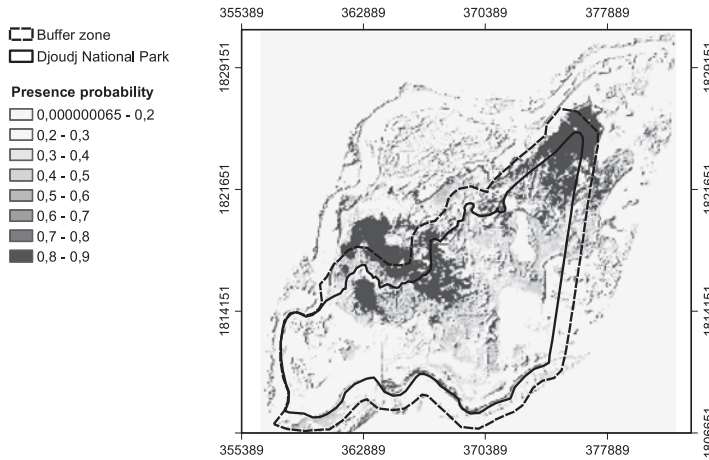


Figure 7. Prediction of presence probability of the Baillon's Crake within the Djoudj area.

and establish new home ranges. This behaviour should be taken into consideration for the design of studies investigating e.g. densities of rail species based on capture-recapture data.

Habitat selection

On the population level, our regression models confirmed that the occurrence of Baillon's Crakes in the floodplains of the Senegal River delta is positively correlated to rather low and dense vegetation types such as *S. littoralis* while tall and rough-textured stands such as *T. australis* have an explicit negative effect both on abundance as well as presence probability. This finding is in accordance with previous observations of Baillon's Crakes in European breeding grounds selecting for fine-stemmed vegetation and avoiding extensive reed-beds and cattail stands (Noll 1924, Szabó 1970). Furthermore, Baillon's Crakes were generally less abundant in vegetation dominated by species which do not provide adequate cover such as *E. mutata* and *S. maritimus*. While monospecific stands of *E. mutata* can form impenetrable and flat layers when plants collapse due to wind and decreasing water levels, *S. maritimus* grows more sporadically, often forming loose stands with poor cover, especially in lower depressions with high water levels (Tegetmeyer *et al.* 2014, N. Seifert unpubl. data).

Variables expressing heterogeneity in vegetation composition were included both in the logistic as well as Poisson model, revealing increasing presence probability and abundance with increasing edge length of patches of *O. longistaminata* as well as *E. mutata* and *T. australis*, respectively. All selected vegetation types have in common that transition between different specific patches is quite distinct. *O. longistaminata* often forms monospecific and very dense stands with its leaves forming a continuous overhead cover, resulting in well-defined edges at the transition to other bordering stands. The same effect is observed for small patches of *E. mutata*, especially when collapsed, while stands of *T. australis* interspersed into bulrush- and grass-dominated habitats indicate areas of rather sparse vegetation with a high proportion of open water and thus also distinct edge structures. The importance of edge structures in Baillon's Crakes' habitat selection was also reflected on the individual level, manifested in second order habitat selection by selective use of the land cover classes "path" and edge length of water bodies by radio-tracked birds in the study sites GL and TG.

Preferences for edges have been identified in several habitat selection studies of bird species inhabiting comparable habitats such as Aquatic Warbler *Acrocephalus paludicola* (Tanneberger 2008), Reed Warbler *A. scirpaenus*, Marsh Warbler *A. palustris* and Sedge Warbler *A. schoenobaenus*

(Surmacki 2005). Likewise, the composition of home ranges of King Rails revealed selection of microhabitat based on distance to open water and plant species richness (Pickens and King 2013) and studies of foraging behaviour of Clapper Rails indicated extensive use of emergent marsh edges (Clark and Lewis 1983, Zembal and Fancher 1989, Rush *et al.* 2010). Most studies explain this pattern with a better food supply, as structural as well as micro-climatic conditions near edges are more favourable for many invertebrates (Voigts 1976, Kaminski and Prince 1981) with e.g. dipterans being blown over the lower area and stopped in front of higher vegetation stands, while Odonata may use such boundaries for spatial guidance (Baldi and Kisbenedek 1999). Rehm and Baldassarre (2007) found especially the interface between vegetation and open water an important parameter explaining abundance of several marsh bird species such as Sora Rail and Virginia Rail as well as the American Bittern *Botaurus lentiginosus* and Least Bittern *Ixobrychus exilis*. In contrast to the aforementioned studies, the authors consider the reduction of intraspecific competition is due to visual isolation of territorial birds by a spatially complex pattern of interspersed vegetation and water as the main reason promoting increased breeding densities.

In the two study sites GL and TG, invertebrate abundances especially of Brachycera, Coleoptera and Saltatoria were found to be significantly higher at vegetation edges (Seifert *et al.* 2015). Accordingly, it seems likely that food availability is an important factor for Baillon's Crakes leading to disproportionate use of edge structures. It can also be speculated whether the smaller home range sizes found for TG are a response to higher heterogeneity (plant species richness, edge structures) of the study site, potentially providing higher food supplies. This would be comparable to Pickens and King (2013) who found home ranges of Clapper Rails being smaller and movements significantly shorter when 95% kernels contained greater amounts of small, interspersed water bodies. However, based on our rather small sample size and the unclear reproductive status of radio-tracked birds, other underlying factors such as reduced intra-specific competition could not be investigated in this study and therefore cannot be excluded here.

Interestingly, in second order habitat selection, only *E. mutata* stands in GL were significantly selected among vegetation types by radio-tracked birds. Beside those patches providing invertebrate-rich edge structures, the plant fraction of Baillon's Crakes' diet was found to consist almost exclusively of seeds of *E. mutata* (Seifert *et al.* 2015), indicating that this plant species also provides an important component of the birds' diet. Furthermore, fresh stalks of the plants may be used as nesting material as the majority of nests in GL were found in small patches of *E. mutata* (N. Seifert unpubl. data). As most individuals did not clearly select any other vegetation type, we hypothesise that in second order selection representing home ranges, structural characteristics of vegetation are generally more important for Baillon's Crake habitat selection than plant species composition.

Third order habitat selection revealed rather low selection levels with only relocation of individuals at GL being disproportionately more associated with edges along water bodies. Apart from this, individual ratios showed on the one hand strong differences in selectivity between animals, resulting in wide confidence intervals and non-significant global selection ratios. On the other hand, ratios were distributed close to 1, indicating little difference in individual use and resource availability within the home ranges. Several explanations may account for this apparent lack of (consistent) selectivity. Firstly, in hierarchical selection analyses there may well be levels already too high to detect differences in usage and availability as major selection has already been made on a lower level (Johnson 1980, Thomas and Taylor 1990). Accordingly, the smallest scale in selection considered in this study might be below the smallest scale at which Baillon's Crakes (in our study design) perceive and respond to habitat structure (Kotliar and Wiens 1990). Secondly, however, due to the rather low number of relocations obtained for most of the radio-tracked birds, we were not able to delineate core areas which could have revealed stronger patterns of selectivity within the home ranges by identifying and weighing repeated usage of certain habitat structures.

Furthermore, owing to its strong seasonal dynamics water level was not considered in our analyses, although this parameter is most probably of major importance and influences all levels

of habitat selection of Baillon's Crakes (B. Taylor pers. obs.). Especially in TG, where some areas of the study site fell dry in the course of the season, birds were forced to constrict their whereabouts to remaining patches which were still water-logged. Thus, availability of some habitat structures may have been more restricted than we were able to account for in our study design.

Habitat suitability and population size estimate

Based on our models, we predicted the extent of suitable habitat in the Djoudj area to comprise 9,516 ha (95% CI 3,138–19,166 ha). However, these numbers should rather be interpreted as a potential maximum extent, as water level could not be included in our models. In practice, water levels in the floodplains decrease from approximately mid-November on (Schwöppe *et al.* 1991), after the closure of sluices usually around mid-October (I. Diop *in litt.*). Thus, the effective size of suitable area diminishes in the course of the dry season until almost all shallowly inundated sites are dry by March (N. Seifert, C. Tegetmeyer pers. obs.). However, the gradual reduction of habitat size may not be linear as Baillon's Crakes seem to prefer intermediate water levels from 10 to 30 cm (Taylor and Van Perlo 1998, Franke 2013, Seifert 2015) and some formerly deeply flooded sites in the centre of the National Park may become suitable rather late during the season while others are already completely dry by then.

Our population density model predicted a population size of 10,714 Baillon's Crakes (95% CI 3,146–17,408) within the study area. Referring to the potential extent of suitable habitat, this would result in a density of 0.90–1.12 birds*ha⁻¹ which is of the same magnitude as our home range size estimates with a mean of 1.77 ha suggests. Assuming that one home range comprises one breeding pair and does not overlap substantially with home ranges nearby, densities would constitute 0.88 birds*ha⁻¹. Abundance data for Baillon's Crakes both in breeding as well as non-breeding habitats are scarce with only Taylor (unpubl. data 1997 in Taylor and Van Perlo 1998) reporting a minimum of 2 birds*ha⁻¹ in a breeding site in South Africa and densities of 4 birds*ha⁻¹ for non-breeding birds in Kenya. A sole observation of 41 birds*ha⁻¹ indicates that the species can potentially occur in very high densities, at least outside the breeding season (Taylor and Van Perlo 1998). Against this background our estimates seem rather low. However, data from study sites where birds were repeatedly captured during the field season indicate that densities vary clearly between sites and years (N. Seifert unpubl. data). Thus, Baillon's Crakes are most probably not homogeneously distributed throughout the habitats in the Djoudj area. Furthermore, decreasing water levels may force the birds to gather in sites which are still inundated, leading to potentially increasing densities towards the end of the season.

In general, comparison of abundance data of rallid species might be futile as numbers are often reported to be highly variable. The population of Spotted Crakes in Biebrza Valley can differ by 90% (Schäffer 1994) between years. Jenkins *et al.* (1995) estimated the population density of Water Rails *Rallus aquaticus* to sum up to 14 birds*ha⁻¹ while Brambilla and Rubolini (2004) inferred breeding densities of 1.85 birds*ha⁻¹. As the controlling factor governing abundance of crakes is often specified to be water level (e.g. Koshelev 1994, Schäffer 1999, Pickens and King 2013, B. Taylor pers. comm.), we assume that the size of the Baillon's Crake population in the Djoudj area may also vary substantially between years owing to inter-annual differences in water regime, governed by factors such as meteorological conditions as well as the hydrological management of the PNOD.

Significance of the Djoudj and the Senegal River Delta

Owing to the species' secretive behaviour and erratic occurrence, population estimates for Baillon's Crake should be considered highly tentative and certainly erroneous. The official projection by BirdLife International (2015) assumes a global population size of 8,700–25,000 mature individuals, while some national population estimates are already up to 100,000 breeding

pairs (e.g. China; Brazil 2009). For Africa, only a few population estimates exist with Taylor (1997) assuming the South African breeding population to consist of 5,400 breeding pairs, while Wetlands International (2016) extrapolate a total of 10,000–25,000 individuals for Eastern and Southern Africa including Madagascar. Accordingly, based on these strong uncertainties it is impossible to infer the proportion of the global (or at least African) population for which the Djoudj area might serve as habitat. However, with a potential of 9,500 ha of suitable wetlands, the PNOD and the Senegal River Delta might be of outstanding importance for African and possibly also European populations of the Baillon's Crake. Although connectivity between European breeding sites and the Senegal River Delta has still not been fully understood, Seifert *et al.* (2016) suggested that the Djoudj area as well as adjacent floodplains in the delta (e.g. Diawling NP) could possibly be regarded as a source, playing an important role for the maintenance of the declining breeding populations in Europe.

Moreover, our discovery of a quite substantial but so far entirely overlooked population calls the reliability of recent population size assessments for Baillon's Crake into question. Most of the national estimates are considered to be of medium or poor quality (BirdLife International 2015) or do not exist at all. It seems likely that there might be further important refuges whose relevance for the species are not yet sufficiently recognised. However, for a sound inference of e.g. the conservation status of the Baillon's Crake it is indispensable to improve the baseline data both by intensification of field surveys and e.g. comprehensive modelling approaches to counteract the difficulties in recording this evasive species. Especially for West African wetlands such as the Inner Niger Delta, Mali, which are increasingly influenced and altered by agricultural utilisation and hydroelectric power production, further research is necessary to investigate potential occurrence of the species and enhance population estimates for the region.

Implications for habitat management

It is well established that habitats need to be sufficiently inundated as a prerequisite for the occurrence of Baillon's Crake (Taylor and Van Perlo 1998). Accordingly, providing appropriate water levels throughout the (breeding) season is the key measure in managing the species' habitats. Therefore, water levels between 10 and 30 cm should be targeted as these levels allow a dense growth of the typical sedge or bulrush dominated vegetation. However, the establishment of monospecific stands should be avoided as diversity of both plant species and habitat structure increases the abundance of invertebrate food and thus habitat suitability. Small-scale structures such as open water bodies or bare soil, trampling paths and a mosaic of higher and lower vegetation can be generally achieved and maintained by a low-intensity livestock grazing scheme with e.g. wetland adapted cattle. In some habitats prone to succession, grazing also reduces the invasion of plant species with unfavourable growth structure such as *Typha* or *Phragmites* spp. and can prevent the shift of wetland margins into shrub communities. However, as cattle grazing in wetland habitats can be problematic due to increased risk of erosion through excessive trampling and overgrazing as documented for many African wetlands (e.g. Driver *et al.* 2011), intensity, length and timing of the grazing period need to be carefully managed. For some regions and habitats, controlled burning can be an alternative way to sustain favourable vegetation composition and structure (e.g. McWilliams *et al.* 2007). At some latitudes, though, effects of burning have to be carefully considered as biomass from the previous year provides essential cover during the onset of the breeding season (T. Wulf, W. Heim pers. comm.).

Supplementary Material

To view supplementary material for this article, please visit <https://doi.org/10.1017/S0959270917000077>

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