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Habitat use and niche separation in Kingfisher species in the Pacific lowlands of Costa Rica

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Abstract. Four kingfisher species can be observed throughout the year along rivers in the southern Pacific lowlands of Costa Rica. These closely related species forage mainly on fish but also on other aquatic organisms. Because of their similar prey and foraging behavior we expected to find at least weak evidence for niche separation, in order to avoid interspecific competition. From May to July 2010 a total of 33 stream kilometers in vicinity of the Tropical Research Station La Gamba were surveyed for kingfishers. For each individual we recorded its sex, age and its exact geographical position. Furthermore, we measured or estimated various parameters of perching sites. Additionally a variety of habitat parameters were measured along surveyed streams on two different spatial scales, 100 m und 400 m river sections. Because the American Pygmy Kingfisher was only seen once, it was excluded from all data analyses. The remaining three species differed significantly in density (birds/stream km) and size of territories. The smallest species, the Green Kingfisher, was most abundant and occupied the smallest territories, whereas the largest Ringed Kingfisher had the lowest density and the largest territories. The three species also differed significantly in perch height. The largest species (Ringed Kingfisher) preferred higher perches than the two smaller co-occurring species, Amazon and Green Kingfisher. Due to multicollinearity of habitat parameters a principal component analysis was calculated. The five best principal components were tested for effects on kingfisher occurrence on the two different spatial scales using generalized linear models. We only found weak evidence that the quantified habitat variables differentially affected the occurrence of the three kingfisher species along streams and rivers. Our study confirms the theory that the density of predators is negatively correlated with body size. The largest kingfisher, certainly depending on bigger prey, occupied larger territories and therefore had a lower density, than the smaller species. Otherwise, besides different perch height preferences, our data does not indicate prominent niche segregation in the three studied kingfisher species, at least during the non-breeding season.

Keywords: Interspecific competition, stream parameters, perch site selection, body size, territory density, territory size, *Chloroceryle americana, Chloroceryle amazona, Megaceryle torquata*

Zusammenfassung. Vier Eisvogelarten können das ganze Jahr über entlang von Flüssen im Pazifischen Tiefland Costa Ricas beobachtet werden. Die nahe verwandten Arten ernähren sich hauptsächlich von Fisch, jedoch werden auch anderen aquatische Organismen genutzt. Auf Grund ihrer Ähnlichkeit hinsichtlich der genutzten Beutetiere und Fouragierverhalten ist mit einer gewissen Nischendifferenzierung zu rechnen, um interspezifische Konkurrenz zu vermeiden. Von Mai bis Juli 2010 wurden Eisvögel entlang von 33 Flusskilometern in der Umgebung der Tropenstation La Gamba erfasst. Für jedes Individuum wurden Geschlecht, Alter, die genaue geographische Position sowie verschiedene Eigenschaften der Sitzwarte aufgenommen. Zusätzlich wurden verschiedene Habitatparametern entlang der untersuchten Flussstrecken auf zwei unterschiedlichen räumlichen Skalen erhoben, 100 m und 400 m lange Flussabschnitte. Da der Erzfischer nur einmal festgestellt werden konnte, wurde er in keiner der statistischen Analysen berücksichtigt. Die drei verbleibenden Arten unterschieden sich signifikant hinsichtlich Dichte (Individuen/Flusskilometer) und Größe ihrer Territorien. Die kleinste Art, der Grünfischer, war am häufigsten und besetzte die kleinsten Territorien, wohingegen der große Rotbrustfischer die geringsten Dichten und größten Territorien aufwies. Des Weiteren unterschieden sich die Arten signifikant in der Höhe ihrer Sitzwarten. Die größte Art (Rotbrustfischer) bevorzugte höhere Ansitzwarten als die beiden kleineren Arten Grün- und Amazonasfischer. Aufgrund der hohen Multikollinearität der erhobenen Habitatvariablen wurde eine Hauptkomponentenanalyse gerechnet. Die fünf besten Hauptkomponenten wurden mittels verallgemeinerter linearer Modelle auf Effekte betreffend das Vorkommen der Eisvögel auf den beiden unterschiedlichen räumlichen Skalen getestet. Die Ergebnisse liefern nur sehr schwache Hinweise, dass die verschiedenen Kombinationen von Habitatvariablen unterschiedliche Effekte auf die drei Eisvogelarten zeigen. Unserer Studie bestätigt die Theorie, dass die Dichte von

Prädatoren negativ mit der Körpergröße korreliert. Der größte Eisvogel, welcher auf größere Beute angewiesen ist, besetzte größere Territorien und wies daher eine geringere Dichte als die beiden kleineren Arten auf. Abgesehen von Unterschieden in der Höhe der Ansitzwarte, liefern unsere Daten keine Hinweise auf eine nennenswerte Nischentrennung der untersuchten Arten, zumindest nicht außerhalb der Brutzeit.

Schlagwörter: Interspezifische Konkurrenz, Flussparameter, Sitzwartenpräferenz, Körpergröße, Territoriendichte, Territoriengröße, *Chloroceryle americana, Chloroceryle amazona, Megaceryle torquata*

Introduction

Due to the competitive exclusion principle species competing for the same resources cannot stably coexist if other ecological factors are constant. One of the competitors will always overcome the other, leading to either the extinction of this competitor or an evolutionary or behavioral shift towards a different ecological niche (Townsend et al. 2003). Pronounced differences in body mass of species co-occuring in the same habitat and belonging to the identical feeding guild may indicate reduced competition due to the exploitation of food items of a different size. For example, the preferred fruit size in frugivorous pigeons or the selected prey size in piscivorous birds is usually related to the consumers' body mass (Diamond 1975; Reynolds and Meslow 1984; Samraoui et al. 2012).

In sympatric waterbird species niche segregation or resource partitioning can occur through differences in foraging behavior, dietary specialization, habitat use or morphology (Buckton and Ormerod 2008; Samraoui et al. 2012). Pronounced differences in body mass in co-occurring kingfisher species may indicate reduced competition due different prey size selection (Remsen 1991). However, particularly in simple linear habitats such as shorelines reducing competition only by species-specific prey size selection may be limited due to a reduced number of possible exploitation methods (Orians and Willson 1964). Therefore, differences in body size may be not sufficient for effective niche segregation. Indeed, kingfisher species occurring along shorelines proved to differ not only in exploited prey size but additionally showed species-specific preferences for river width, river depth, stream velocity and perch height (Reyer et al. 1988; Monadjem et al. 1994; Libois and Laudelout 2004; Bonnington et al. 2008; Kasahara and Katoh 2008). Furthermore, larger species feeding on larger prey are expected to need larger areas in order to find enough food, as larger prey is less abundant (Schoener 1968). As a consequence, the average density of a species should decrease with increasing body size (Cotgreave 1995; Krüger 2000; Gaston and Blackburn 2000; Carbone 2002).

In this study, we compared habitat preferences as well as territory density and size of kingfisher species (family Alcedinidae) which can be found along rivers in the southern Pacific lowlands of Costa Rica, the American Pygmy Kingfisher *Chloroceryle aenea*, the Amazon Kingfisher *C. amazona*, the Green Kingfisher *C. americana* and the Ringed Kingfisher *Megaceryle torquata* (Garrigues and Dean 2007). The last three are known to occur in the same habitat and occasionally even nest on the same riverbank (Skutch 1957). All four species feed mainly on fish and other aquatic organisms (Fry et al. 1992). The American Pygmy Kingfisher (APK) is the smallest (13 cm from tip of bill to tip of tail) of the four species. In Costa Rica it is uncommon in the lowlands, where it favors swamp forest, mangrove and shaded streams (Garrigues and Dean 2007). This kingfisher occurs along rivers and streams in forests, while the other three species prefer freshwater habitats in woodland areas (Woodall 1991). The Green Kingfisher (GK) with an average body length of 18 cm is found in almost all open freshwater and brackish habitats (Fry et al. 1992). The Amazon Kingfisher (AK) has an average body size of 28 cm and is common along lowland rivers, streams, pounds, lakes and lagoons (Garrigues and Dean 2007). The Ringed Kingfisher (RK) is the largest (41 cm) of the four kingfisher species and can be found along rivers and streams, lakes, lagoons and large ponds (Garrigues and Dean 2007). An additional species occurring in the southern Pacific lowlands of Costa Rica, the Belted Kingfisher *Megaceryle alcyon*, was not considered in this study. This North American species only occurs as migrant and locally common winter resident in Costa Rica (Fry et al. 1992) and therefore was not present during our survey period (May-July).

Due to similar habitat requirements and feeding modes of the four kingfisher species co-occurring in our study area in the Pacific lowlands of Costa Rica, we expect that a certain extent of niche separation, in terms of perch height preferences and habitat use, will be found to facilitate the avoidance of interspecific competition. Furthermore, we expect the smaller species to be most abundant as well as occupying smaller territories due to their preference for smaller fish, which are available in higher densities (Remsen 1991).

Methods

Study area

The study was conducted in the Pacific lowlands of the Golfo Dulce Region, southern Costa Rica, in vicinity of the Tropical Research Station La Gamba (N 08°42"61', W 083°12'97"; 70 m above sea level; http://www.lagamba.at/researchdb/pagede/index.php). The study area is located between the margin of the Piedras Blancas National Park in the west and the Transamerican Highway in the east (Fig. 1). The annual precipitation at La Gamba is about 6000 mm, with a peak from August to November, and a drier period from January to March. The mean annual temperature is 28.5 °C (Weissenhofer and Huber 2008).

Kingfishers were surveyed along a total river and stream length of 33 km. Considered rivers in our study area represent order 1, 2 and 3 streams of varying width and velocity (Tschelaut et al. 2008). The runoff of rainforest streams in Costa Rica has a strong seasonal variation, as well as a short-term variability in flow, depending on the rainfall (Schiemer and Tschelaut 2010).

Because preliminary surveys have shown that kingfisher species are largely absent from closed forests in our study area (Schulze, unpublished), we only considered streams and rivers embedded in cultivated and other strongly modified habitats such as young secondary forests (Fig. 1). Many river and stream stretches are bordered by gallery forest strips of various width, age and structural complexity. These gallery forest strips are a prominent landscape structure in the southern Pacific lowlands and are protected by the national forestry law (Seaman and Schulze 2010). Occasionally the rivers are flanked by plantations of African oil palm (*Elaeis guineensis*), which are simply structured and have a low plant diversity (Weissenhofer et al. 2008). The open area is mainly characterized by pastures dominated by grasses, Cyperaceae and weeds, which are used for cattle breeding. Further habitats bordering rivers and streams are abandoned or swampy pastures, annual cultures (mainly rice) and timber plantations (Weissenhofer et al. 2008).

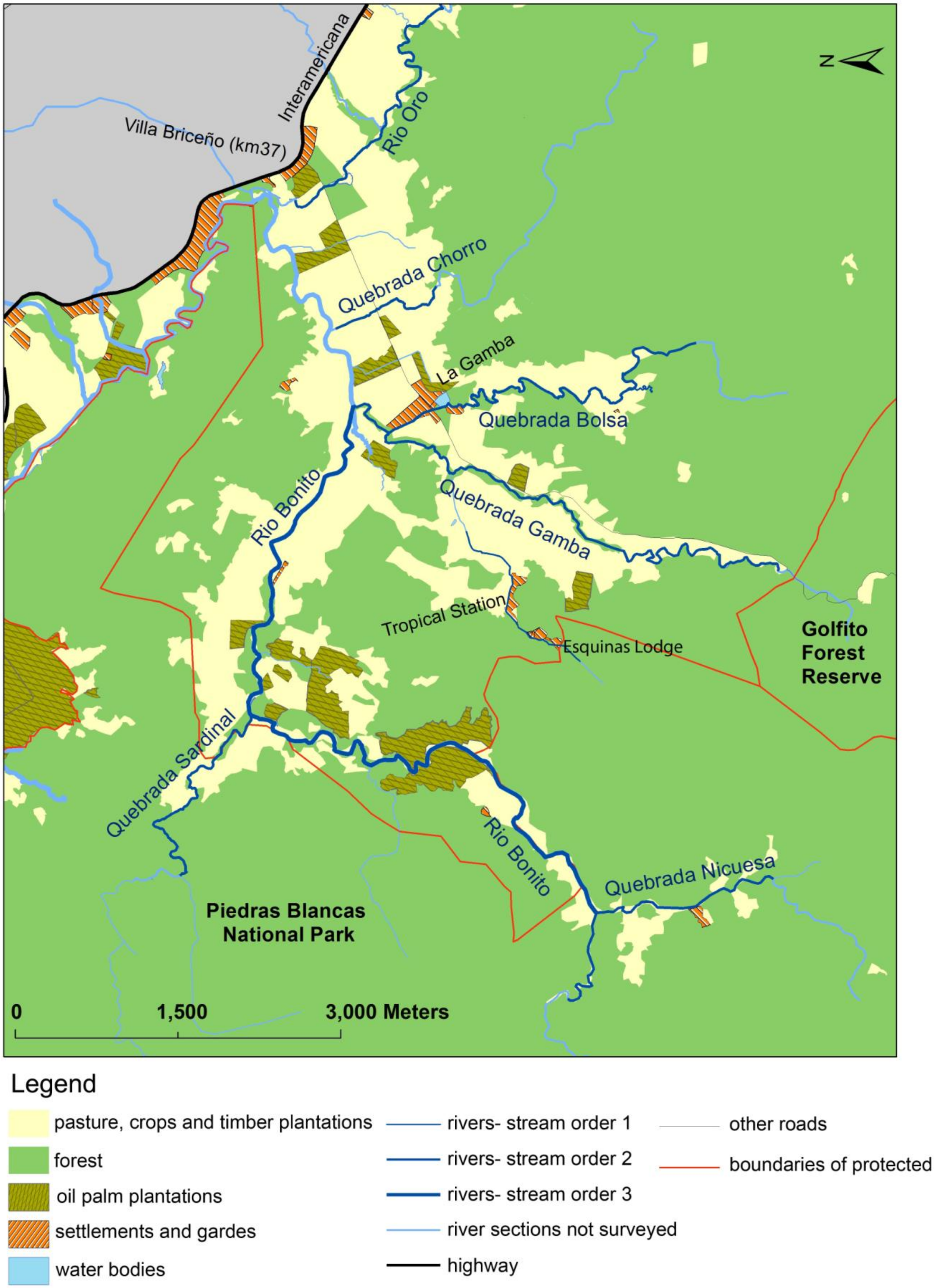

Figure 1. Study area around the Tropical Research Station La Gamba (N 08°42"61', W 083°12'97", 70 m a.s.l.). Gray areas are situated outside the study area.

Kingfisher survey

Kingfisher surveys took place from 6 May–30 July 2010. Surveys started in the morning between 7 and 8 a.m. and lasted until afternoon or until it started to rain (usually at noon or early afternoon). The activity of kingfishers declines during and after rain due to the decreased visibility of prey in turbid water (Bonnington et al. 2008). Kingfishers where surveyed by walking in rivers and streams or on their banks. Each river and stream stretch was surveyed four times. Kingfishers are usually well visible along rivers and streams while perching or flying along the water course. Species, sex and age of observed kingfishers were identified according to Garrigues and Dean (2007).

The location of each kingfisher observation (including perching and flying individuals) was marked on the GPS device (Magellan-Mobile Mapper 6). Additionally, exact observation time and, for perching birds, perch type were recorded. Most perches were branches of alive or dead trees or scrubs. Twice a GK could be observed perching from a big rock and once from the edge of a steep sandy river bank. A few times kingfishers (mainly GK) were seen perching from man-made structures such as fence posts and power supply lines.

When an individual was obviously observed more than once during the same survey, the record was noted as double count. In addition, for flying birds the point where they changed flight direction (most likely at the margin of their territories) was marked on the GPS device to estimate territory boundaries and sizes.

Perching site variables

For each perching site several parameters were measured, which are listed in Table 1. Turbidity, which was measured in several other studies (e.g. Reyer et al. 1988), was neglected because visibility in the streams and rivers of La Gamba is generally very good, and the bottom of the water body was always visible (except after heavy rain when no fieldwork was conducted). To reduce pseudo-replication to a minimum, perching site parameters were not measured or estimated again, when the same individual was obviously observed earlier on the same survey day.

Table 1. Measured parameters at kingfisher perching sites.

Variables	Unit of measurements	Method
Perch height	m	Measured with tape measure or estimated when >2 m
Maximum water depth	cm	Measured with tape measure at the deepest part of river
Water depth at river/stream shoreline	cm	Measured with tape measure in a distance of 1 m from the shoreline/perching site
River/stream width	m	Measured with rangefinder (Nikon Laser 800 S) or estimated when rangefinder did not work (under bad light conditions)
River/stream velocity	s/10m	Measured as time a stick needed to travel 10 m downstream (Bonnington et al. 2008)
Availability of pools	Categories	0 = no pools present, 1 = pools available
Availability of fish[1]	Categories	0 = no fish present, 1 = fish present
Slope of shoreline	Categories	1 = flat, 2 = moderately steep, 3 = steep
Vegetation cover at shoreline	Categories	1 = only herb layer, 2 = scrubs, 3 = scattered trees, 4 = forest
Canopy cover	%	Canopy cover was estimated in % sky covered by vegetation using pictures taken below kingfisher's perching sites from close to ground level into the sky (with a Panasonic DMX- LX3)

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[1] Additionally the body size of all observed fish has been classified as 0-5 cm, >5-10 cm, >10-15 cm and >15 cm. However, because the vast majority of fish belonged to the size group 0-5 cm, the size classification was not used in further analyses.

Habitat variables measured to characterize river and stream stretches

A total of 10 habitat parameters were also measured for every 100 m stream transect for the entire study area. (1) The stream velocity was measured once in the middle of the 100 m transect. For all other variables 100 m transects were subdivided into 10 m sections and variables were measured or estimated for every 10 m section. (2) Maximum water depth, (3) water depth at shoreline and (4) river width were measured in the middle of every 10 m section. Subsequently the means per 100 m transect were calculated and used for further analyses. (5) Availability of pools and (6) fish density were classified between 0 (no pools and fish, respectively, in any of the 10 m transect sections) and 10 (pools and fish, respectively, observed in all 10 m sections of the 100 m transect). Fish density was probably the variable with the biggest error as time was restricted and many fish are hiding under overhanging vegetation, roots, etc. However, these fish may be also not available as prey for hunting kingfishers. For (7) the slope and (8) the vegetation structure at the shoreline, the same categories as in Table 1 were used. Then, the means were calculated for all 100 m transects. In addition, (9) the presence of gravel or sand banks was scored between 0 (none) and 10 (present in all ten 10 m sections of the 100 m transect). Finally, (10) the availability of perches was estimated. Perches were defined as structures such as trees, scrubs, big rocks and branches in the water, based on observations of perching kingfishers during the first bird surveys. Perch availability was also classified in categories from 0 (no perches in any 10 m section) to 10 (perches available in all 10 m sections).

In addition the values of four adjacent 100 m sections were combined into one 400 m section. For parametric variables means were then calculated based on forty 10 m sections, for categorical variables scores ranged from 0-40. To quantify habitat variables for stream sections of different length allows evaluating if the importance of habitat variables for kingfisher species varies with the considered spatial scale.

Territory density and size

If the density of a species is low, recording the location of individual birds over a certain number of visits should result in distinct clusters on the map, each representing the location of a territory (Bibby et al. 2000). This was the case with the species AK and RK.

In contradiction, GK apparently had a high territory density often resulting in a dense packing of territories without obvious gaps between them. Because aggressive confrontations between territory neighbors could be observed very rarely (only once!), the construction of territories on a map was more challenging. We tried to estimate territory boundaries based on observations of the same bird on different locations within one survey. For example, when a kingfisher was flushed by the observer, flew towards the survey direction and did not turn again, a bird of the same species, sex and age observed during the next minutes further up- or downstreams (depending on the survey direction) was classified as the same individual. Furthermore, we noted turning points of individuals flying along rivers and streams (Davis 1982). However, still, not all territory bounders could be clearly defined and in several cases it remained doubtful if observations represent one territory or two neighboring territories. Therefore, for all species we provide a minimum and maximum number of territories and a minimum and maximum territory density (number of territories per river/stream km). ArcGIS 10 (Esri) was used to create a map with the identified territories.

Due to the dependence of kingfishers on the linear shapes of streams and rivers, territory size was quantified as the length of a river/stream stretch occupied by one pair (Davis 1982; Sullivan et al. 2006). To calculate a species' mean territory size, only "conservatively" estimated territory boundaries were considered. Meaning, when a bird adjacent but outside a so far identified territory could not be clearly assigned to it, we did not expand the territory boundary but retained the smaller estimated territory size. Therefore, our territory estimates may underestimate the true mean territory sizes of the surveyed kingfisher species.

Statistical analysis

All data analysis was conducted using the program Statistica 7.1 (Statsoft Inc., Tulsa). Habitat variables were tested for normal distribution and – if necessary – adequate data transformations (log x, arcsin ($\sqrt{x}$)) were carried out. Perch height was transferred into a categorial variable with six categories (0-1 m, >1-2 m, >2-3 m, >3-4m, >4-5 m and >5 m). To test for differences of measured parameters between the three kingfisher species Kruskal-Wallis ANOVAs, one-way ANOVAs (with subsequently LSD tests) and Chi-square tests were calculated. To account for multiple comparisons subsequently a Bonferroni correction was applied.

Due to the high multicolinearity of habitat variables principal component analyses (PCAs) were calculated for 100 m and 400 m river sections, using standardized variable values. Perch availability was not further considered in any subsequent analyses due to its extremely low variance. With the five best principal components (PCs) generalized linear models (GLMs) were calculated for every species for 100 m as well as for 400 m stream/river sections. Incidence data was used for all species in the 100 m river sections and for AK and RK in the 400 m river sections. Therefore, GLMs with binominal error distribution and a logit-link function were calculated. Due to the high density of GK, abundance data (excluding double counts and over flying birds) was used for this species for 400 m river sections. Therefore, GLMs relating the abundance of GK to the five PCs were calculated with a normal error distribution and a log-link function. For each species and both river section lengths GLMs were calculated including all PCs and all possible subsets and then ranked according to their corrected Akaike information criterion (AICc). AICc weights were calculated for those models within 2 AICc values of the model with the lowest AICc, serving as a measurement of support for the model. A high AICc weight, indicates a high relative likelihood of a model compared to other models (Wagenmakers and Farrell 2004).

Results

Abundance and territory densities

Our kingfisher surveys resulted in a total of 508 observations (including over flying birds and double counts) of four different species, APK, GK, AK and RK. APK was only seen once during the study period and, therefore, was excluded from all further analyses. With 326 individuals (excluding double counts) GK had the highest abundance and territory density (Table 2, Fig. 2a), followed by AK with 78 individuals and an intermediate territory density (Table 2, Fig. 2b). RK was only recorded 47 times and had the lowest territory density (Table 2, Fig. 2c). All three species were found along all rivers and streams, expect Quebrada Negra, a very small and narrow stream, and at a small side arm of Quebrada Gamba, where only GK was observed (for site names compare Fig. 1). Territory size (log x transformed) differed significantly between all three kingfisher species (one-way ANOVA: $F_{2,40} = 18.51$, $p < 0.001$; Table 2, Fig. 3).RK occupied the largest territories, GK had the smallest territories. An intermediate territory size was found for AK (Table 2, Fig. 3).

Table 2. Total number of observed individuals (excluding double counts), total number of 100 m river/stream sections with records, number of identified territories, territory density and mean territory size of Green Kingfisher (GK), Amazon Kingfisher (AK) and Ringed Kingfisher (RK)..

Species	**Number of observations**			**100 m river/stream sections with records**	**Number of territories[1]**	**Territories per stream km [1]**	**Mean territory size ± SD [stream km]**
	total	**♂♂ (juv.)**	**♀♀ (juv.)**				
GK	326	130 (9)	122 (9)	182	26 (-33)	0.79 (-1)	0.76 ± 0.19
AK	78	20 (1)	33	68	9 (-14)	0.27 (-0.42)	1.10 ± 0.31
RK	47	23	6	42	8 (-9)	0.24 (-0.27)	1.60 ± 0.67

[1] Numbers in brackets consider all potential territories.

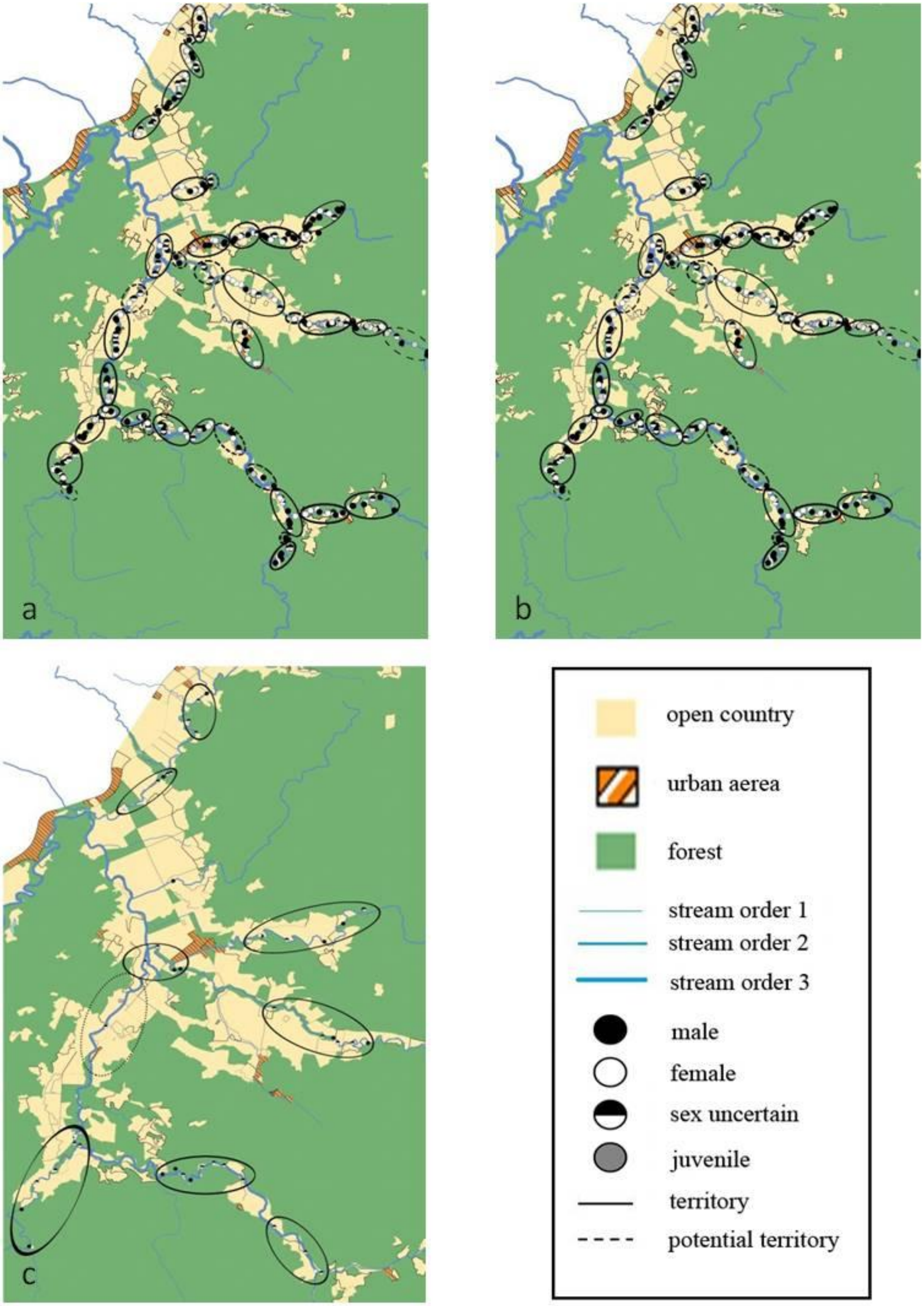

Figure 2. Maps indicating territories as well as age and sex of observed birds for (a) Green Kingfisher, (b) Amazon Kingfisher and (c) Ringed Kingfisher.

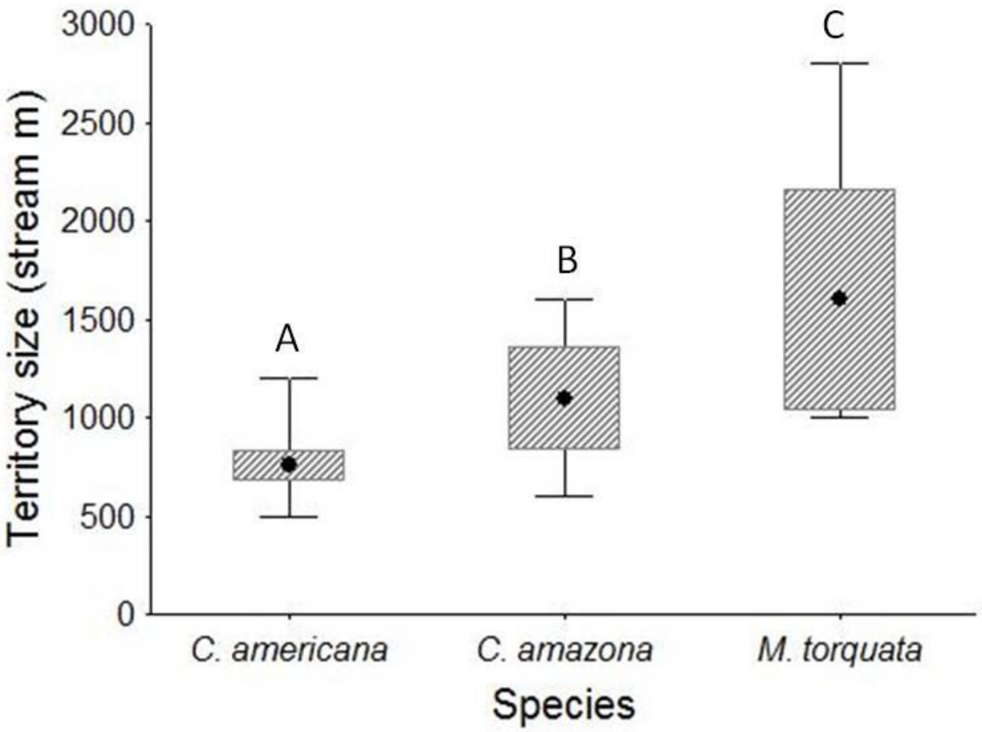

Figure 3. Mean territory size ± 0.95 confidence interval (box) and min-max. (whiskers) of the Green Kingfisher (*C. americana*), the Amazon Kingfisher (*C. amazona*) and the Ringed Kingfisher (*M. torquata*). Different letters indicate significant differences (LSD tests).

Species-specific characteristics of perching sites

For these analyses only perching kingfishers were considered. Perch height proved to differ between the three kingfisher species, even after applying a Bonferroni correction. All other variables did not show a significant difference (Table 3). The GK had the lowest mean perch height and the RK the highest (Fig. 4).

Table 3. Results of univariate tests for differences of measured perch site parameters between the three kingfisher species. Significant differences are printed bold.

Variables	Statistical tests	Results
Perch height categories	Kruskal-Wallis ANOVA	**$H_2 = 76.79$, $p < 0.001$**
log (stream width (m))	one-way ANOVA	$F_{2,284} = 0.99$, $p = 0.371$
log (max. water depth (m))	one-way ANOVA	$F_{2,284} = 1.66$, $p = 0.192$
log (water depth below perch (m))	one-way ANOVA	$F_{2,284} = 1.11$, $p = 0.332$
Slope categories	Kruskal-Wallis ANOVA	$H_2 = 0.42$, $p = 0.811$
Fish incidences	Chi-square test	$\chi^2 = 4.83$, $p = 0.089$
log (velocity)	one-way ANOVA	$F_{2,284} = 0.87$, $p = 0.419$
Shoreline vegetation	Kruskal-Wallis ANOVA	$H_2 = 0.97$, $p = 0.617$
arcsin (√(canopy closure/100))	one-way ANOVA	$F_{2,284} = 1.26$, $p = 0.285$

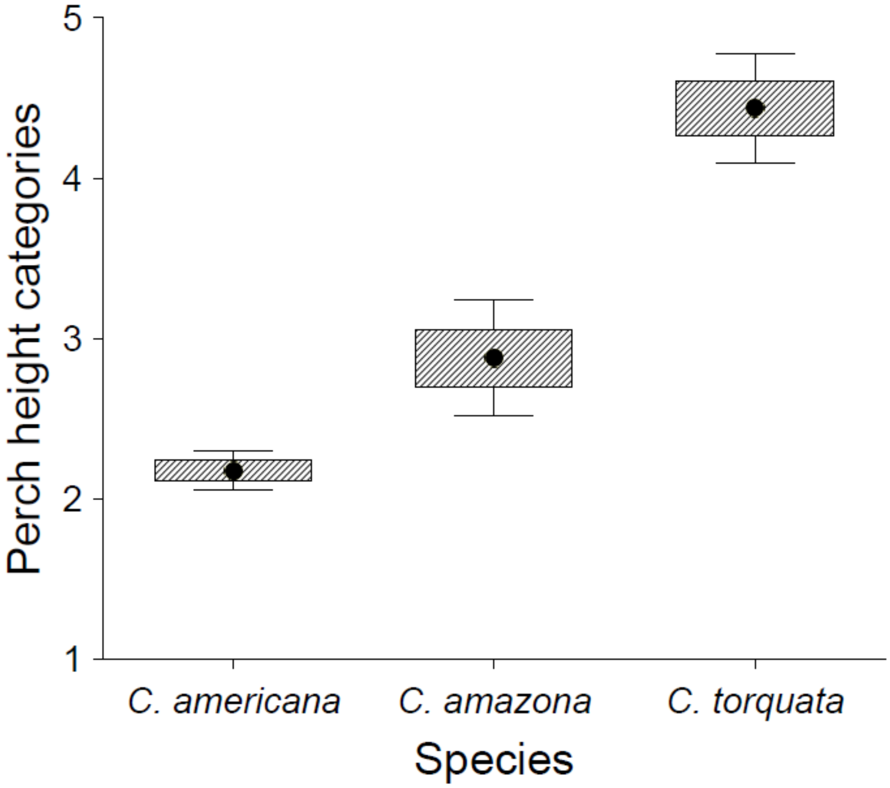

Figure 4. Mean perch height categories ± SD (box) and 95% CI (whiskers) of the three kingfisher species.

Habitat variables

Spearman rank correlations indicate a high degree of multicolinearity of the ten predictor variables for 100 m and 400 m river sections (Appendix Table A and B). Combining all variables using a PCA (excluding perch availability due to its extremely low variance), the first five PCs of the PCA explain 72.51% of the variance of the original variables for 100 m river sections and 85.35% for 400 m river sections (Table 4). PC 1 was related to stream width, max. water depth, mean water depth, and shoreline vegetation for both spatial scales, while PC 2 explained best the variablity of mean shoreline slope and shoreline vegetation for 100 m river sections and the variability of mean shoreline slope and fish abundance for 400 m river sections. PC 3 was highly related to flow velocity on both spatial scales and to fish abundance for 100 m sections. PC 4 has a close correlation with the occurrence of pools for 100 m sections and with the occurrence of sandy river banks for 400 m sections. PC 5 was related to the occurrence of sandy river banks on both spatial scales (Table 5).

Table 4. Explanatory power and variance of the first five factors of a PCA on all predictor variables for 100 m and 400 m river sections.

PC	Explanatory power	% total var.	Accumulated explanatory power	Accumulated %
		100 m river sections		
1	2.40	26.67	2.40	26.67
2	1.65	18.31	4.05	44.98
3	1.10	12.24	5.15	57.22
4	1.00	11.16	6.16	68.39
5	0.91	10.12	7.07	72.51
		400 m river sections		
1	2.93	32.60	2.93	32.60
2	1.72	19.15	4.66	51.75
3	1.26	13.97	5.91	65.72
4	0.99	11.03	6.91	76.75
5	0.77	8.60	7.68	85.35

Table 5. Results of principal component analyses on stream variables (standardized) calculated separately for 100 m and 400 m river sections. Grey cells indicate a close correlation between the stream variable and the respective principal component ($r \geq 0.50$).

Variables	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**
100 m river sections					
Sandy river bank	0.28	-0.41	-0.17	-0.39	0.60
Flow velocity	0.06	-0.03	-0.76	0.44	-0.28
Stream width	0.63	0.23	0.23	-0.11	-0.14
Max. water depth	0.91	-0.26	-0.01	-0.03	-0.11
Mean water depth at shoreline	0.82	-0.41	-0.05	0.05	-0.18
Mean shoreline slope	-0.20	-0.80	-0.06	-0.14	-0.20
Shoreline vegetation	-0.59	-0.52	-0.18	-0.21	-0.08
Pools	-0.04	0.34	-0.18	-0.75	-0.49
Fish abundance	0.22	0.41	-0.61	-0.18	0.34
400 m river sections					
Sandy river bank	0.23	0.49	-0.08	0.51	-0.66
Flow velocity	-0.02	-0.43	-0.78	0.18	0.08
Stream width	0.81	0.09	0.14	-0.12	0.08
Max. water depth	0.89	0.33	-0.14	-0.00	0.13
Mean water depth at shoreline	0.83	0.34	-0.25	-0.04	0.20
Mean shoreline slope	-0.35	0.58	-0.46	0.11	0.27
Shoreline vegetation	-0.70	0.46	-0.19	0.10	0.12
Pools	0.09	-0.18	0.40	0.80	0.40
Fish abundance	0.32	- 0.69	-0.37	0.17	-0.14

Habitat preferences

The five best PCs from the PCAs (compare Table 5) were used to calculate GLMs testing for effects on kingfisher occurrence in 100 m and 400 m sections. Only for GK on the scale of 400 m river sections abundance data were used due to the species' high density.

According to Wald statistics (Appendix Table C), only PC3 has a significant effect on the occurrence of the GK in 100 m river sections and is also the only variable which remained in the eight best models (Table 6). That indicates that flow velocity and fish abundance (compare Table 5) might have an influence on the species' habitat preference. Stream width, maximum water depth, mean water depth at shoreline and shoreline vegetation are the parameters best explained by PC1, which is the only variable occurring in all the five best models for AK (Table 7) and significantly affected the species' occurrence in 100 m river sections according to Wald statistics (Appendix Table D). None of the five PCs had a significant effect on the occurrence of RK in 100 m river sections according to Wald statistics and none of the calculated GLMs achieved a significant level (results not shown).

Table 6. Results of GLMs including all PCs (compare Table 5) and all possible subsets testing for effects on occurrence of the Green Kingfisher in 100 m stream sections. Only models within 2 AICc values of the model with the lowest AICc are shown. Variables with a significant contribution according to Wald statistics (Appendix Table C) are printed bold.

Variables included	**Df**	**AICc**	**AICc weight**	***P***
PC3	1	363.70	0.124	0.007
PC2 + **PC3**	2	364.03	0.105	0.011
PC3 + PC4	2	364.21	0.096	0.012
PC2 + **PC3** + PC4	3	364.40	0.088	0.013
PC3 + PC5	2	364.61	0.079	0.014
PC2 + **PC3** + PC5	3	364.90	0.068	0.016
PC3 + PC4 + PC5	3	364.90	0.068	0.016
PC2 + **PC3** + PC4 + PC5	4	365.13	0.061	0.016

Table 7. Results of GLMs including all PCs (compare Table 5) and all possible subsets testing for effects on occurrence of the Amazon Kingfisher in 100 m stream sections. Only models within 2 AICc values of the model with the lowest AICc are shown. Variables with a significant contribution according to Wald statistics (Appendix Table D) are printed bold.

Variables included	**Df**	**AICc**	**AICc weight**	***p***
PC1	1	307.27	0.185	0.005
PC1 + PC4	2	307.82	0.141	0.010
PC1 + PC2	2	308.63	0.094	0.015
PC1 + PC5	2	308.93	0.081	0.017
PC1 + PC2 + PC4	3	309.18	0.071	0.019

PC2 had a significant effect on the abundance of GK in 400 m river sections according to Wald statistics (Appendix Table E) and is also the only variable contained in the two best models (Table 8). PC2 is best explained by mean shore line slope and fish abundance (compare Table 5). No GLM achieved a significant level when testing for effects of the five PCs on the occurrence of AK within the 400 m river sections (results not shown). For RK, PC2 appeared affecting weakly its occurrence in 400 m river sections. It was the only variable which remained in the five best models. However, PC2 did not significantly affect its occurrence according to Wald statistics (results not shown) and even the best GLMs hardly achieved a significant level (Table 9).

Table 8. Results of GLMs including all PCs (compare Table 5) and all possible subsets testing for effects on the abundance of the Green Kingfisher in 400 m stream sections. Only models within 2 AICc values of the model with the lowest AICc are shown. Variables with a significant contribution according to Wald statistics are printed bold.

Variables included	**Df**	**AICc**	**AICc weight**	***P***
PC2	1	280.39	0.271	0.003
PC2 + PC4	2	281.88	0.130	0.008

Table 9. Results of GLMs including all PCs (compare Table 5) and all possible subsets testing for effects on occurrence of the Ringed Kingfisher in 400 m stream sections. Only models within 2 AICc values of the model with the lowest AICc are shown. There are no variables with a significant contribution according to Wald statistics.

Variables included	Df	AICc	AICc weight	*P*
PC2	1	87.33	0.157	0.042
PC1 + PC2	2	87.88	0.119	0.057
PC2 + PC3	2	88.95	0.070	0.097
PC2 + PC4	2	89.00	0.068	0.109
PC2 + PC5	2	89.25	0.060	0.113

Discussion

Abundance and territory densities

Only three kingfisher species were abundant enough in our study area to analyze their perch site and habitat preferences. The fourth species, the APK, was only observed once in three months. It is the rarest species in the lowlands of Costa Rica (Garrigues and Dean 2007). However, its density may be underestimated due to its preference for more shaded habitats compared to the other three species (Willard 1985; Remsen 1991). Therefore, the APK may be more difficult to detect. Also the species' escape behavior may contribute to a decreased likelihood of detection. When disturbed, APKs tend to escape into the shade of nearby vegetation cover, whereas the other three species escape by following the river flying over open water, where they are easily detectable (Remsen 1991). However, even when considering such differences in detectability, it appears to be without doubt, that the APK has an extremely low density in our study area. This may reflect that most surveyed river and stream stretches are located in open areas. Only short stretches are bordered by dense secondary forest with a canopy partly overhanging and thereby shading the river shorelines, which is the preferred habitat of the APK (Remsen 1991).

In many species their density or abundance decrease with increasing body size and weight (Cotgreave 1995; Gaston and Blackburn 2000; Krüger 2000; Carbone 2002;

Damuth 2007). In birds this relationship is strongest in carnivorous species such as raptors (Juanes 1986). Although other ecological factors like competition (Cotgreave 1995; Carbone 2002), prey density (Carbone 2002) and the availability of nesting sides (Juanes 1986) play an important role too, the population density of larger carnivorous species is mainly limited by their demand of larger territorries or home ranges. This is an important precondition to find or monopolize enough food (Krüger 2000), as for predators the amount of acceptable and accessible food in biomass per area decreases with increasing weight of the consumer due to usually lower densities of larger prey (Schoener 1968). Besides the APK, which is by far the smallest and rarest kingfisher species in our study area (0.03 birds per stream km), the other three species followed the expected body size-abundance relationship. The most abundant GK (2.7 birds per stream km) represents the smallest of the three species, while the largest RK was the rarest species (0.40 birds per stream km) in our study area. AK showed an intermediate density (0.63 birds per stream km). At a small stream in Bolivia, where the same kingfisher species (except APK) were present, RK was also the rarest (0.67 individuals per stream km) and GK the most abundant species (1.50 birds per stream km); AK was characterized by an intermediate density (0.78 birds per stream km; Remsen 1991). However, densities of the species considered in our study can vary enormously and cannot always be explained by differences in body size, as reported by Remsen (1991) from other study sites in Columbia and Bolivia. Such differences may be caused by a varying complexity of freshwater habitats. While the average stream width in our study area was 10.92 m (ranging between 1.9 m and 39 m), several of the streams surveyed by Remsen (1991) were wider, connected to adjacent lakes during the rainy season, bordered by adjacent floodplain forest or partly covered with floating vegetation.

It is known that kingfishers are highly territorial in the breeding season but much less is known about territoriality after the offspring left the parental territory. The GK is laying eggs between February and April (Stiles and Skutch 1989; Hoyo et al. 2001) and it takes about two and a half month before the young birds become independent (Hoyo et al. 2001). Males and females of the GK were observed several times together or at least at the same site (but during different surveys), and with associated young birds, especially at the beginning of the survey period. In most of the defined territories both sexes were present.

This provides evidence that both sexes are staying together in a territory throughout the whole year.

The AK is laying eggs between January and March (Stiles and Skutch 1989; Hoyo et al. 2001) and the young birds leave the nest at the earliest 21 days later (Davis and Graham 1991). Therefore, it is likely that most of the young birds already have left the parental territory before our survey started in May. Only one juvenile bird could be recorded during the survey period. Perhaps, plumage differences between juveniles and adults have been largely disappeared at this time of the year. According to Skutch (1957), it is not unlikely that both sexes of AK stay together in their territory throughout the year. During our study, at least in four of the identified territories a male and a female were present, although we could never observe both sexes at the same time. It was also mentioned by Skutch (1957) that even when both sexes use the same territory throughout the year, they are rarely seen together. In addition there is one territory where only a female was present throughout the survey period and several where whether the territory bounder or the sex is certain.

The RK is laying eggs between March and May (data for Panama; Hoyo et al., 2001). Young birds leave the nest 57 days later (Hoyo et al. 2001). Nevertheless, in our study area no juvenile birds could be recorded even at the beginning of the survey. However, for many of the observed individuals determination of age and sex was not possible, as they escaped before getting a good view on them. At least in three identified territories both sexes were observed. For all other territories, it is very likely that they were shared by both sexes, as very often two birds where observed together but sex determination was not possible. To summarize, our observations provide clear evidence that in all three kingfisher species both sexes occupy a territory together throughout the whole year, as it is the case in most kingfishers (Fry et al. 1992).

Habitat preferences

For kingfisher species preying on aquatic organisms from perches, the location and height of perches may have major effects on successful foraging. In our study area, the three surveyed kingfisher species showed pronounced differences in preferred perch heights. The GK used a mean perch height of 2.2 m, while the AK perched slightly higher (average perch height: 2.8 m) and the RK had the highest mean perch height of 4.5 m. Perch heights of 2.8 and 4.1 m documented for AK and RK, respectively, by Remsens (1991) for a study site in Columbia are identical (AK) or very similar (RK) to the perch heights found in our study, while the perch height of 1.22 m found for the GK was lower than the height found at La Gamba. This is not really surprising as preferred perch heights differs significantly between studied areas (Remsen 1991). Possible reasons are a different availability of perch types or a different fish size distribution, which would force kingfishers to adapt their optimal perch heights (Remsen 1991). The overall availability of perches along streams and rivers in our study area was generally very high and therefore not further considered in our habitat models.

Effects of habitat variables, which were considered in our study, on the different kingfisher species were generally weak (GK, AK) or could not be detected (RK). On the scale of 100 m river sections PC3 (best explained by flow velocity and fish abundance) had a week effect on the occurrence of the GK, while on the larger scale of 400 m river sections the species' abundance was significantly related to PC2 (best explained by mean shoreline slope and fish abundance). The occurrence of AK in 100 m river sections proved to be significantly affected by PC1 (best explained by stream width, max. water depth, mean water depth at shoreline and shoreline vegetation). Due to the generally low AICc weights indicating a low explanatory power of the calculated models, we do not further discuss the potential importance of individual habitat variables. However, we like to emphasize that our results provide at last weak evidence that the importance of different combinations of habitats varies between species and spatial scales. In principal, most variables highly related to PCs, which were significantly related to the occurrence or abundance of the two kingfisher species, such as shoreline vegetation, fish abundance, water body features and shoreline slope proved to affect habitat suitability of kingfishers in other studies (e.g. Remsen 1991; Reyer et al. 1988; Sullivan et al. 2006; Kasahara and Katoh 2008). Furthermore, we did not consider habitat structures such as suitable nesting sites. Kingfishers nest in sandy riverbanks (Fry et al. 1992), which are always located in steep shoreline sections. However, as the study was conducted during the non-breeding season, we did not find any nesting activity indicating which riverbanks represent suitable nesting sites.

In general, it seems that all three studied Neotropical kingfisher species do not have highly specialized habitat requirements. At least the habitat parameters measured in this study only had little or none influence on their occurrence or abundance in surveyed river sections. GK, AK and RK all occur along shorelines of lakes and rivers as well as in mangrove forests (Stotz et al. 1996). As long as perches, enough prey and adequate nesting sites are available they seem to be rather tolerant against other changing environmental conditions. As mentioned earlier, perches did not appear to be a limiting factor in our study area. Even in short river sections free of vegetation on its shorelines, stones and dead branches in the water could be used as perches. However, as many of these structures were not exposed very high, perch availability could be a limiting factor for the large RK.

Niche segregation

It can be assumed that three sympatric species that live in the same habitat and have a similar feeding mode, as the three kingfisher species GK, AK, and RK in our study, show a certain extent of niche segregation and resource partitioning in order to avoid interspecific competition. Besides differences in preferred perch heights, the three kingfisher species did not differ in any other of their perching site characteristics.

Species-specific perch height preferences were already reported for Neotropical kingfishers studied in Peru, Bolivia and Columbia (Willard 1985; Remsen 1991), for African kingfisher species (Monadjem et al. 1994; Libois and Laudelout 2004; Bonnington et al. 2008) as well as for kingfishers occurring in Japan (Kasahara and Katoh 2008). Differences in perch heights can indicate species-specific exploitation of prey of different size. At a study site in Colombia the GK, the smallest species using the lowest perches, used prey of a mean length of 19.4 mm, the largest species, the RK, used the highest perches and hunted the largest prey with a mean length of 91.0 mm. The intermediate-sized AK was characterized by an intermediate perch height and feed on prey with an average length of 42.8 mm (Remsen 1991). Similar patterns were found in African (Libois and Laudelout 2004; Bonnington et al. 2008) and Japanese Kingfisher communities (Kasahara and Katoh 2008). By selecting different perch heights, kingfishers of different size can maximize their capture ratio. The lower the perch, the smaller the observable water surface area. However, the higher the perch, the more difficult is the detection of prey items. Small species have to perch near the water surface as they feed on small prey which is harder to detect but more abundant so that a smaller range of vision might be sufficient. Bigger species can use higher perches, as bigger prey is still detectable from a larger distance, and therefore have the advantage of a larger observable radius (Remsen 1991). By optimizing perch height, different sized kingfishers are able to maximize surveillance of appropriately sized prey (MacArthur 1972).

There are several studies documenting that closely related species that occur in the same area and use similar resources differ in size and consequently exploit different food. This is for example the case with sympatric tropical skinks (Manicom and Schwarzkopf 2011), as well as with fruit doves, where smaller doves use smaller fruits than larger species (Diamond 1975). This may effectively decrease interspecific competition, as documented for coexisting raptors like *Accipiter* and *Circus* species. Again, in these raptors larger species hunt larger prey than smaller species (Reynolds and Meslow 1984; Krüger 2000; Garcia and Arroyo 2005). According to Hutchinson (1959) a mass ratio of 1:1.3 is sufficient to reduce competition between two potential competitors, assuming that animals that vary that much in size would feed on different sized prey. As the ratio between the body weights of the three observed kingfisher species is by far larger than 1:1.3 (GK : AK = 1:2.75; AK : RK = 1:2.72; data on body weight from Hoyo et al. 2001) it is most likely that prey size is a very important factor for niche segregation.

In contrast to the studies on African (Libois and Laudelout 2004; Bonnington et al. 2008) and Japanese (Kasahara and Katoh 2008) kingfishers we could not find differences in water depth and stream width at perch sites between the three studied kingfisher species. In other studies larger kingfisher species preferred deeper water at broader stream sections, where they hunted sometimes by hovering over the water. Although hovering behavior during hunting is also reported for GK, AK and RK (e.g. Skutch 1957; Stiles and Skutch 1998; del Hoyo et al. 2001), in our study area kingfishers usually hunted from perches on the shoreline of surveyed streams and rivers. Therefore differences in water depth may be less important.

Kingfishers almost completely rely on fish within the first few centimeters below the water surface and seldom immerse completely. Hunting near the surface has the advantage of higher success rates because the fish have less time to detect the predator. Furthermore, kingfishers can access prey with a lower energetic effort and decrease the risk of being caught by predatory fish (Reyer et al. 1988; Remsen 1991). To summarize, water depth may be not an important factor as long as there are enough fish of appropriate size available close to the water surface. However, bigger kingfisher species may need deeper water in order to reduce the chance of injury (Bonnington et al. 2008).

Synopsis

The three kingfisher species GK, AK and RK, which were studied in the Pacific lowlands of southern Costa Rica, differed most obviously in their preference for different perch heights, while only weak differences in species-specific preferences for other habitat variables could be found. However, it has to be considered that our study was conducted during the non-breeding season. Niche segregation may be more obvious during the breeding season, a time period with an increased demand for food resources and with the necessity of access to suitable nesting sites.

During the non-breeding season interspecific competition does apparently not play an important role for shaping the small kingfisher community at our study area. During our three-month survey we did not observe any interspecific interactions and often two different species were perching close to each other. The mechanism for this “peaceful co-existence” still remains largely unknown. Perhaps the availability of the two important resources food and nesting sites does not act as limiting factor in tropical kingfishers, at least when species show a sufficient difference in body size and preferred perch heights, both facilitating exploitation of different food sources.

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Appendix

Table A. Results (r_s values) of Spearman rank correlations for habitat variables measured in 100 m river sections. Significant correlations ($p < 0.05$) are indicated by grey cells.

Variable	**(1)**	**(2)**	**(3)**	**(4)**	**(5)**	**(6)**	**(7)**	**(8)**	**(9)**
Sandy river bank (1)		0.02	-0.04	0.17	0.16	0.24	0.10	-0.08	0.08
Flow velocity (2)			-0.14	-0.12	-0.04	0.07	0.16	0.03	0.10
Stream width (3)				0.52	0.35	-0.21	-0.39	0.10	0.10
Max. water depth (4)					0.89	-0.01	-0.31	-0.02	0.15
Mean water depth at shoreline (5)						0.13	-0.23	-0.08	0.06
Mean shoreline slope (6)							0.46	-0.07	-0.23
Shoreline vegetation (7)								-0.02	-0.12
Pools (8)									0.14
Fish abundance (9)									

Table B. Results (r_s values) of Spearman rank correlations for habitat variables measured in 400 m river sections. Significant correlations ($p < 0.05$) are indicated by grey cells.

Variable	**(1)**	**(2)**	**(3)**	**(4)**	**(5)**	**(6)**	**(7)**	**(8)**	**(9)**
Sandy river bank (1)		-0,07	0.00	0.22	0.18	0.23	0.09	0.13	-0.04
Flow velocity (2)			-0.23	-0.27	-0.19	0.07	0.11	0.02	0.34
Stream width (3)				0.77	0.56	-0.35	-0.56	0.09	0.25
Max. water depth (4)					0.93	-0.07	-0.38	0.08	0.15
Mean water depth at shoreline (5)						0.04	-0.32	0.03	0.13
Mean shoreline slope (6)							0.59	-0.14	-0.40
Shoreline vegetation (7)								-0.05	-0.43
Pools (8)									0.10
Fish abundance (9)									

Table C. Results of Wald statistics from univariate analyses of five principal components (PC1-5) (resulting from a PCA on habitat variables) in GLMs testing for effects on the occurrence of the Green Kingfisher in 100 m river sections. Significant results ($p < 0.05$) are indicated by grey cells.

Effect	**df**	**Wald Statistic**	***p***
Constant	1	22.57	<0.001
PC 1	1	0.04	0.836
PC 2	1	1.82	0.177
PC 3	1	6.25	0.012
PC 4	1	1.84	0.175
PC 5	1	1.34	0.247

Table D. Results of Wald statistics from univariate analyses of five principal components (PC1-5) (resulting from a PCA on habitat variables) in GLMs testing for effects on the occurrence of the Amazon Kingfisher in 100 m river sections. Significant results ($p < 0.05$) are indicated by grey cells.

Effect	**df**	**Wald Statistic**	***P***
Constant	1	67.28	<0.001
PC 1	1	7.56	0.006
PC 2	1	0.74	0.389
PC 3	1	0.04	0.850
PC 4	1	1.50	0.221
PC 5	1	0.37	0.541

Table E. Results of Wald statistic statistics from univariate analyses of five principal components (PC1-5) (resulting from a PCA on habitat variables) in GLMs testing for effects on the abundance of the Green Kingfisher in 400 m river sections. Significant results ($p < 0.05$) are indicated by grey cells.

Effect	**df**	**Wald Statistics**	***p***
Constant	1	218.06	<0.001
PC 1	1	0.001	0.975
PC 2	1	9.92	0.002
PC 3	1	0.02	0.879
PC 4	1	0.55	0.458
PC 5	1	0.02	0.894

Lebenslauf

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Ausbildung

1997-2005	BRG Rosasgasse, 1120 Wien (Matura mit ausgezeichnetem Erfolg)
Seit 2005	Diplomstudium Biologie in Wien, Studienrichtung Ökologie
Seit 2010	Diplomarbeit mit ornithologischem Thema am Department für Tropenökologie und Biodiversität der Tiere. 3 Monate Freilandarbeit im Regenwald der Österreicher in Costa Rica: Kartierung von Eisvögeln und Aufnahme von Habitatparametern.

Sonstige Tätigkeiten im Bereich Biologie

Seit 2009	Ökopädagogin bei den Naturfreunden Wien und dem Verein Umwelt Spürnasen

Praktische Erfahrung

2011/12	Teilnahme an verschiedenen ornithologischen Kartierungen
07 und 08/2012	Mithilfe auf den Beringungsstationen Hohenau-Ringelsdorf (Österreich) und Lake Annsjön Birdobservatory (Schweden)

Sprachkenntnisse	Deutsch (Muttersprache) Englisch (sehr gut) Spanisch (mäßig)