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SHORT COMMUNICATION

Effect of individual incubation effort on home range size in two rallid species (Aves: Rallidae)

Jan Jedlikowski[1] · **Mattia Brambilla**[2,3]

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Abstract Home range varies with individual traits, environment, and time, but studies relating variations to behavioural traits are scarce. We investigated variation in home-range size in nesting rallids in relation to incubation effort, sex, weight, available space, and food abundance. In Water Rail, individuals more involved in incubation had smaller home-ranges, regardless of sex, whereas in Little Crake both parents incubate with similar effort, and the main factor positively affecting home-range size was available space. Results suggested that home-range size during the nesting period may vary according to incubation behaviour, especially in species with high inter-individual variation in incubation effort.

Keywords Incubation behaviour · Nest attentiveness · Radio-tracking · *Rallus aquaticus* · *Zapornia parva*

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✉ Jan Jedlikowski
janjedlikowski@biol.uw.edu.pl

1 Faculty of Biology, Biological and Chemical Research Centre, University of Warsaw, Żwirki i Wigury 101, 02-089 Warsaw, Poland

2 Fondazione Lombardia per l'Ambiente, Settore Biodiversità e Aree protette, Largo 10 luglio 1976 1, 20822 Seveso, MB, Italy

3 Sezione Zoologia dei Vertebrati, Museo delle Scienze, Corso della Scienza e del Lavoro 3, 38123 Trento, Italy

Zusammenfassung

Effekte individuellen Bruteinsatzes auf die Größe von Home-Ranges bei zwei Rallen-Arten

Die Größe eines Home-Range ("Streifgebiet") ist bestimmt von individuellen Eigenschaften des Vogels, Umwelt und Zeit, aber Untersuchungen zu Zusammenhängen zwischen Größe des Home-Range und Verhalten sind selten. Wir untersuchten Unterschiede in der Größe der Home-Range bei brütenden Rallen im Vergleich zum Bruteinsatz, Geschlecht, Gewicht, verfügbarem Platz und Verfügbarkeit von Nahrung. Bei Wasserrallen hatten Individuen, die mehr an der Brut beteiligt waren, unabhängig vom Geschlecht, kleinere Home-Ranges, während beim Kleinen Sumpfhuhn, bei dem beide Eltern mit ähnlichem Einsatz an der Brut beteiligt sind, die Größe der Home-Ranges positiv korrelierte mit dem verfügbaren Platz. Die Ergebnisse legen nahe, dass die Größe von Home-Ranges während des Brütens vom Brutverhalten bestimmt ist, besonders bei Arten mit großen individuellen Unterschieden im Einsatz für die Brut.

Introduction

The extent of the home range may be determined by the interactions between animal behaviour, environment, and time (Börger et al. 2006). Although home range is a key issue in animal ecology, most studies focused primarily on its physiological or ecological determinants, such as body size, food availability, or population density (McLoughlin and Ferguson 2000), whereas behavioural traits have received little attention (e.g. Hingrat et al. 2004). In this study, we evaluated the effect on home range size of variation in individual incubation efforts, expressed as nest attentiveness, i.e. the percentage of time that a parent sits on the nest and incubates clutch, the most important and time-consuming activity for the vast majority of species which adopt bird-egg contact incubation (Deeming and Reynolds 2015). In birds, incubation is often shared by both parents, and the degree of involvement of both males and females may differ among pairs within and among species (Clutton-Brock 1991). We expected that individuals less involved in the incubation process would have potentially larger home-ranges, as they could spend more time outside the nest, being more involved in other activities, e.g. territory defence or food searching (including for the incubating partner).

We therefore, investigated factors affecting home range size in two Rallidae species, Water Rail (*Rallus aquaticus*) and Little Crake (*Zapornia parva*; formerly *Porzana* genus). These species are characterized by biparental incubation, although in the former the females incubate more consistently than males (Andreas 1996), whereas in the latter both sexes have been reported to spend a similar amount of time at the nest (Dittberner and Dittberner 1990). By investigating this study system, we aim at evaluating the relative importance of individual behaviour (nest attentiveness) and of other potentially relevant ecological traits, as environmental factors (food and habitat availability), and individual traits (body weight, sex).

Methods

The study was conducted in northeastern Poland (Masurian Lakeland) at seven mid-field waterbodies (mean area 2.17 ha), located between 53°48′–53°52′N and 21°37′–21°43′E. All ponds were partly overgrown by emergent vegetation (57–76 %) and surrounded by arable fields, pastures, and fallows (Fig. 1; see also Jedlikowski et al. 2014, 2015).

Fieldwork was carried out in May–June 2011–2012. Telemetry data were collected during the incubation period. We caught 13 Water Rails (belonging to 8 pairs) and 21 Little Crakes (12 pairs). All trapped birds were weighed, sexed, and fitted with a radio-telemetry transmitter (1.5 g, PicoPip Ag392, Biotrack). Tags were glued to small piece of gauze (1-cm^2), and subsequently to feathers on the back of each bird (total weight 1.0–3.3 % of body mass). We started radio-tracking birds after 24 h from fitting transmitters. Birds were tracked every 2 h (enough for birds to freely traverse their entire home-range) for 4 days (day and night), except during periods of heavy rain.

To quantify nest attentiveness of radio-tagged individuals, we used camera traps (5210A-940, LTL Acorn Outdoors) camouflaged at a 1-m distance from the nest, 1 day after the beginning of telemetry data collection. Camera traps recorded incubation constancy and recess frequency during one 24-h period. Nest attentiveness thus refers to the percentage of time over the day spent on nest by an individual.

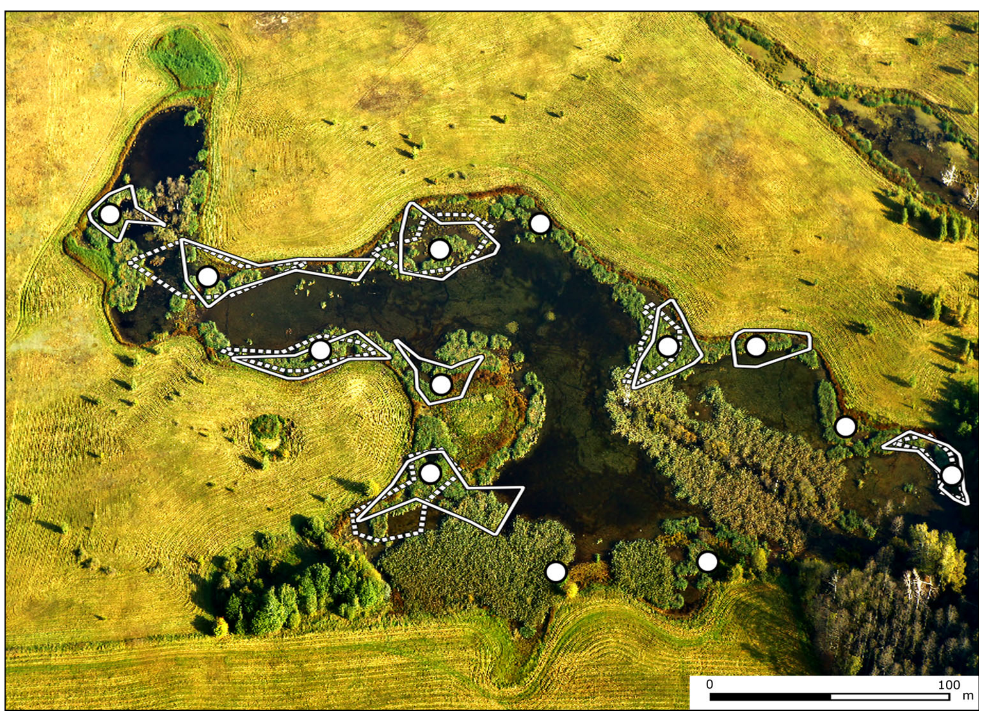

Fig. 1 A typical small water body (5.5 ha) within the Masurian Lakeland agricultural landscape (NE Poland) overgrown by emergent vegetation (mainly bulrush and common reed), and inhabited by 13 pairs of Little Crake (nests marked by *white dots*), 2012 (photo by Krystian Trela). Home ranges (concave polygons) of nine males (*solid line*) and six females (*dotted line*) are shown (see text for details)

The area potentially available for each pair (i.e. free from competitors) was calculated as the area (m^2) of continuous emergent (i.e. neither submerged nor terrestrial) vegetation surrounding the nest of the tracked individual as far as the two nearest adjacent neighbouring nests (hereafter "available space"). To evaluate the potential food availability, we collected food samples (aquatic invertebrates, the most important food resource), from a 10-m radius around the nest of each tracked individual. Ten vertical sweeps (1 m long) with a standard D-shaped invertebrate dip net (ca. 504-cm^2 opening, 1-mm mesh size) were done in the subsurface zone among the emergent vegetation layer. Sampling was carried out 1 day before birds were radiotracked. Macroinvertebrates were preserved in a 70 % ethanol buffer and sorted from the submerged aquatic vegetation within 4 h of sampling. All specimens were subsequently dried at 60 °C for 24 h, weighed to the nearest 0.00001 g, and placed for 2 h in a muffle furnace at 550 °C to burnt off all the organic matter. Subsequently, the ash content was weighed, and the ash-free dry mass of each sample was calculated as dry mass minus the ash content. Ash-free dry mass was taken as an estimate of the potential food availability for rallids.

To estimate the home-range of each specimen, we used the concave polygons method (Kenward 2001), suitable when movement of animals is restricted to particular areas. In our case, both species were strictly tied to wetlands and never occupied terrestrial habitats. Only individuals that generated ≥35 locations were analysed (10 Water Rails: the members of four pairs plus one male and one female; 17 Little Crakes: the members of seven pairs plus three males).

To evaluate the potential effect of the factors considered (Table 1), we built generalized least squares (GLS) models with 100 % concave polygon (CP_{100}) as the dependent variable, and three sets of potential predictors: environmental factors (food availability, available space), individual traits (body weight, sex), and behaviour (nest attentiveness). We compared the explanatory power of each set (and of variables) by means of an information-theoretic approach. We used AIC_C-ranking to identify the most supported models within each type of predictors, and to evaluate what kind of factors (environmental, individual, nest attentiveness) were more likely to affect home-range size. For the final GLS models we provided Nagelkerke's R^2. See Supplementary Material for full Methods.

Results

The average home range size in Water Rails (671.6 m^2 ± 103.7 SE) was 33 % larger than in Little Crakes (447.3 m^2 ± 46.2 SE; $t_{25} = 2.26$, $P = 0.033$).

In Water Rail, nest attentiveness had a negative effect on home range size ($\beta = -14.13 \pm 2.83$, $P < 0.001$; model intercept: $\beta = 1332.82 \pm 157.14$; Fig. 2a) and the relative model was highly supported ($R^2 = 0.67$). For individual traits, the most supported model for CP_{100} included sex (for males: $\beta = 407.55 \pm 260.63$, $P = 0.162$; model intercept: $\beta = 564.11 \pm 1102.80$), but was much less supported than the behavioural model (Table 2). The most supported model in relation to environmental traits was the null model (all other models had $\Delta AIC_C > 2$).

In Little Crake, the available space had a positive effect on the CP_{100} ($\beta = 0.07 \pm 0.03$, $P = 0.025$; model intercept: $\beta = 237.97 \pm 80.60$; Fig. 2b), and the relative model was highly supported ($R^2 = 0.33$). Considering the individual and behaviour traits, the most supported models were the null models (Table 2).

Discussion

We found support for the importance of nest attentiveness (but not for other individual traits) in Water Rails, and for environmental factors (namely available space) in Little Crakes. The relatively high explanatory power of the models suggested that the selected variables were amongst the most relevant to explain the variance in observed home range.

Our results for Water Rails provides direct evidence (for the first time, to our knowledge) that home range size is affected by variations in incubation behaviour (regardless from sex *per se*): individuals spending more time

Table 1 Variables (mean ± SE) used in home-range models, presented separately for Water Rail and Little Crake

Variable	Water Rail		Little Crake	
	Male ($n = 5$)	Female ($n = 5$)	Male ($n = 10$)	Female ($n = 7$)
Nest attentiveness (%)	32.5 ± 3.9 [21–45]	60.1 ± 2.0 [55–65]	51.2 ± 2.1 [41–61]	47.8 ± 2.4 [40–55]
Body weight (g)	140.86 ± 4.54 [128.0–155.8]	119.32 ± 4.51 [104.1–129.2]	53.64 ± 0.70 [50.2–56.3]	53.79 ± 2.52 [45.8–66.0]
Available space (m^2)	6343.0 ± 949.5 [3210–9960]		2399.6 ± 389.3 [1010–6370]	
Food abundance (g)	2.232 ± 0.673 [0.07–4.48]		1.682 ± 0.705 [0.02–9.68]	

Ranges are shown in square brackets

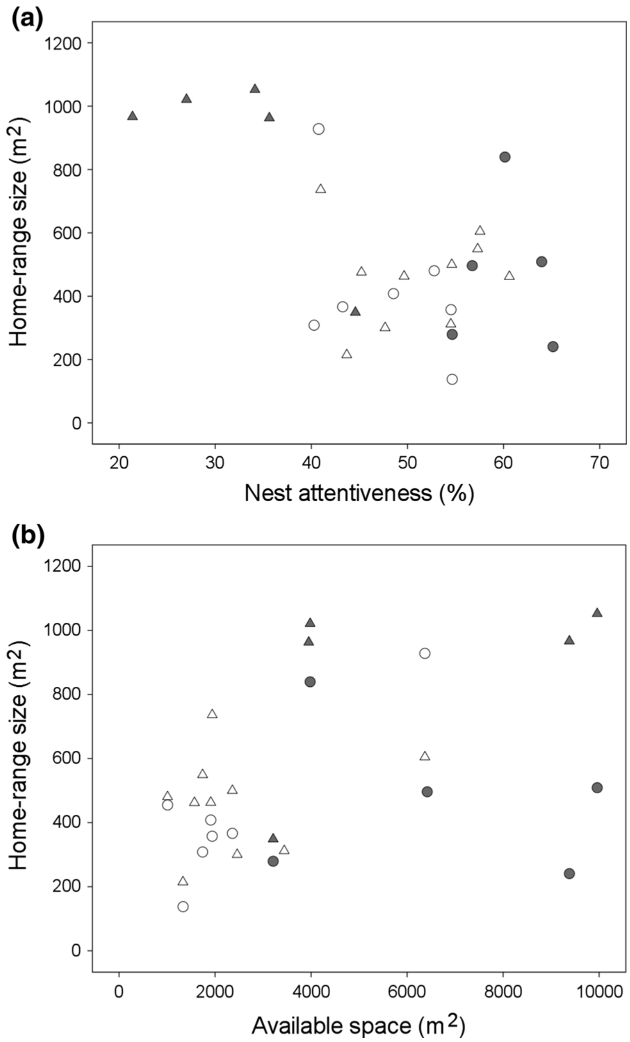

Fig. 2 Relationship between home range size (CP_{100}), nest attentiveness (percentage time spent on the nest by individuals; **a**), and available space (**b**). The former relationship was significant for Water Rail (*grey symbols*), the latter for Little Crake (*white ones*). *Triangle symbols* represent males, *circles* females

incubating clutches have, on average, smaller home ranges. This is consistent with some previous indirect evidence for, e.g., Marsh Harrier (*Circus aeruginosus*) and Black Rail (*Laterallus jamaicensis*), where females, which are more involved in incubation than males, are characterized by smaller home ranges (Cardador et al. 2009; Tsao et al. 2009). It seems reasonable that individuals with higher nest attentiveness have relatively less time for other activities (e.g. feeding or preening), and this in turn may result in smaller home ranges. In Little Crake, where both parents spend similar time incubating clutch, nest attentiveness did not affect home range size.

For Little Crake, the main factor affecting variation in home range size was available space. Little Crake occupied water bodies at a much higher density than Water Rail, and this is the likely reason for such result. Density regulation plays an important role during the process of territory settlement, especially in highly territorial species (López-Sepulcre and Kokko 2005). Rails maintain all-purpose breeding territories, i.e. which have to ensure all ultimate resource needs within inhabited water body (nest site, food, shelter, and mates), and are characterized by intensive antagonistic behaviour expressed not only towards conspecifics, but also towards other species (Taylor and van Perlo 1998). Their territorial aggressions extend most probably to the whole home range area, as the neighbouring home ranges were always clearly separated and never overlapped (see Fig. 1). In Water Rails, we did not find any effect of available space on home range size. However, we expect that also in this species, home range size could be strongly affected by neighbour occurrence especially in sites with higher birds densities. Bengtson (1967) estimated that in area with high Water Rail density (6.4–7.5 pairs/ha), the average size of territories was only 320 m^2 (with maximum up to 590 m^2); therefore, his observed territories were much smaller than those in our study area, where this species nested with a mean density equal to 0.75 pair/ha (Jedlikowski et al. 2014).

Independent of the impact on nest attentiveness, food availability is known to affect home range size by determining the area needed to obtain sufficient energy (McLoughlin and Ferguson 2000). Our models found no effect of invertebrate biomass on the home range sizes of Little Crakes and Water Rails, although such a lack of effect could potentially be explained in (at least) two different ways. First, wetlands are highly productive habitats and, especially in such small water bodies with few or no fish, invertebrate biomass may be relatively high and uniformly distributed among littoral microhabitats (Rennie and Jackson 2005). In this case food abundance may be so high as not to affect home range size. Secondly, our way of measuring the food abundance by sampling macroinvertebrates may not reflect the true extent of the trophic resource that is available to the rallids. This may happen because not all invertebrates may be selected as prey by the two species, or alternatively, they could also rely to some extent on terrestrial invertebrates, plant and other diverse animal material which we failed to sample (Taylor and van Perlo 1998).

In summary, variation in home range size in Water Rails was strongly affected by a behavioural trait, nest attentiveness. There is, however, large variation in incubation pattern and off-nest behaviour among birds; therefore, further studies are required, especially for species with uniparental incubation system and in particular to evaluate the potential importance of off-nest behaviour. We may expect also that a pattern similar to the one we found might be rather common among species where both partners take part to incubation, and which maintain well defended territories (then largely coinciding with home-ranges) used

Table 2 Summary of the GLS models describing home range size (CP_{100}) according to environmental factors (food availability, available space), individual traits (body weight, sex), and behaviour (nest attentiveness) for Water Rail and Little Crake

Model	*df*	logLik	AICc	ΔAIC_C	w_i
Water Rail					
Environmental factors					
Intercept	3	−71.59	153.2	0.00	0.89
Intercept + food availability	4	−71.27	158.5	5.36	0.06
Intercept + available space	4	−71.56	159.1	5.94	0.04
Intercept + food availability + available space	5	−71.07	167.1	13.96	0.01
Behaviour					
Intercept + nest attentiveness	4	−66.07	148.1	0.00	0.93
Intercept	3	−71.59	153.2	5.05	0.07
Individual traits					
Intercept + sex	4	−68.38	152.8	0.00	0.49
Intercept	3	−71.59	153.2	0.42	0.39
Intercept + body weight	4	−69.83	155.7	2.89	0.11
Intercept + sex + body weight	5	−68.38	161.8	8.99	0.01
Little Crake					
Environmental factors					
Intercept + available space	4	−109.44	230.2	0.00	0.65
Intercept	3	−112.28	232.4	2.19	0.22
Intercept + available space + food availability	5	−109.43	234.3	4.10	0.08
Intercept + food availability	4	−112.14	235.6	5.40	0.05
Behaviour					
Intercept	3	−112.28	232.4	0.00	0.80
Intercept + nest attentiveness	4	−111.90	235.1	2.73	0.20
Individual traits					
Intercept	3	−112.28	232.4	0.00	0.61
Intercept + body weight	4	−111.59	234.5	2.12	0.21
Intercept + sex	4	−112.02	235.4	2.98	0.14
Intercept + body weight + sex	5	−111.312	238.1	5.68	0.04

Models are ranked according to Akaike's information criterion corrected for small sample size (AIC_C) and Akaike's weights (w_i)

for mating, nesting, and feeding sites during breeding. For such species, nest attentiveness may be a key determinant of home-range size and may be much more important than other potential predictors.

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