# Sex-specific habitat use by reintroduced Great Bustards in the UK

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Sex-specific habitat use by reintroduced Great Bustards in the
UK

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Reintroduction is an important technique for restoring species, requiring knowledge of animal-landscape interactions for effective conservation management, and differences in habitat requirements between life stages and sexes need to be taken into account. The globally-threatened Great Bustard *Otis tarda* has one of the largest sexual size dimorphisms of any bird species, thus the sexes are expected to have substantially different habitat preferences. Captive-reared individuals have been released in the UK as part of a trial reintroduction since 2004. Here, we investigate the habitat preferences of male and female Great Bustards using Maximum Entropy modelling. The key variables influencing distributions were distance from roads and settlements, and land-use type, consistent with wild populations studied previously elsewhere. We show sex-specific habitat preferences, where males selected habitat based mainly on the distance from human infrastructure, whereas females selected habitat based mainly on land-use type. Females preferred calcareous grassland over arable and horticulture areas, whereas males did not show a preference, reflecting potential sex differences in diet and breeding habitat requirements. Although females were predicted to prefer a higher proportion of the study area in SW England than males, preferred areas for both sexes constituted 17.7%, suggesting that preferred habitats are not limiting. Habitat preference analysis provides essential insights into the behaviour and ecology of reintroduced species, assisting in the identification of areas for targeted habitat management and the selection of future release sites, critical to project success.

Word count: 234

**Keywords:** distribution modelling, farmland birds, grassland, maximum entropy, reintroduction
Reintroduction is an important technique in conservation for restoring depleted species populations, degraded habitats and ecosystems (Butchart et al. 2006; Ewen et al. 2012; Adhikari et al. 2012). Although reintroductions have been shown to be significant in the conservation of some species (Butchart et al. 2006), not all projects have been successful, highlighting the importance of monitoring for providing insights into factors affecting the success of reintroductions (Seddon et al. 2007; Armstrong & Seddon 2008; Sutherland et al. 2010). It can be difficult to assess prior to release how individuals will use their new environment, particularly during the establishment phase when individuals disperse away from the release site into novel, and often unmanaged, areas. Therefore knowledge of animal-landscape interactions is essential for adaptive project management (Carroll et al. 2003; Bar-David et al. 2008; Ewen et al. 2012). Captive-reared individuals may be less successful than wild-born individuals, as they may lack the appropriate cues when selecting habitat due to lack of experience; therefore the study of post-release habitat use is particularly important to guide conservation action (Stamps & Swaisgood 2007; Rantanen et al. 2010).

Effective conservation management requires consideration of the habitat requirements of individuals at all life stages and both sexes. For instance, species distribution models not incorporating sex may bias their estimation toward the more frequently observed sex, underestimating important environmental factors for one sex, while overestimating them for the other (Conde et al. 2010). It may be particularly important to account for this when a species displays sexual segregation or morphological differences between the sexes which could generate different ecological requirements. For example, sexual size dimorphism (SSD), the size difference between males and females, is seen in many taxa and should be an important consideration for conservation management of species that exhibit sex-specific life histories (Hedrick & Temeles 1989; Fairbairn et al. 2007; Székely et al. 2007). SSD has been associated with habitat segregation and differential migration in several taxa, related with
differences in predation risk, reproductive strategies, digestive capabilities, thermoregulatory limitations and intersexual competition (Main et al. 1996; Katsikaros & Shine 1997; Ruckstuhl, 2007; Palacin et al. 2009; Singh et al. 2010). Gray et al. (2009) found males of the sexually-dimorphic and critically endangered Bengal Florican (Houbaropsis bengalensis) preferred burned grassland, while females preferred unburned grassland and dry-season rice head-ponds; conservation of the population requires protection of both male- and female-specific habitats. Disregarding significant intersexual differences in habitat preference modelling will not only reduce the effectiveness of the modelling, but more importantly, the value of consequential conservation management (Bowyer 2004; Foster & Soluk 2006; Safi et al. 2007; Gray et al. 2009; Conde et al. 2010).

Here we focus on the Great Bustard Otis tarda Linneus, a species of steppe and arable habitats, which exhibits one of the largest sexual size dimorphism in body mass of any bird species, with males being approximately 2.4 times the mass of females (Cramp 1980; Raihani et al. 2006; Martin et al. 2007). Sex differences begin early in development, with male chicks having greater energy requirements (Quaisser et al. 1998), consuming a diet with a greater proportion of invertebrates than plant matter (Bravo et al. 2012), and showing faster development than female chicks (Heinroth & Heinroth 1928; Radu 1969; Glutz et al. 1973); these differences are suggested to contribute heavily to the higher first-year mortality of male chicks recorded in the Iberian population (Martin et al. 2007). As adults, Great Bustards show sexual segregation (Cramp 1980; Lane et al. 2001), spending much of the year in single-sex flocks and showing female-only parental care of eggs and chicks, and differential dispersal and distributions (Palacin et al. 2009); therefore we expect habitat preferences to differ between sexes (Mysterud 2000). Studies have suggested that male bustards may select habitat providing abundant food and good visibility, whereas female bustards may show stronger selection for undisturbed areas and those with a good availability of invertebrates.
while nesting and rearing chicks (Moreira et al. 2004). Both sexes in wild populations generally show avoidance of human infrastructure, such as roads, settlements and power lines (Martínez 1991; Lane et al. 2001; Raab et al. 2010; Burnside et al. 2013).

The Great Bustard is globally-threatened, experiencing dramatic declines and local extinctions across its range in the 20th Century due to a combination of hunting, egg-collection and changes in agricultural practice (Palacín & Alonso, 2008). This species became extinct in the UK in the 1830s (Osborne 2005); a 10-year trial reintroduction in South-West England began in 2003, with the first release of birds in the autumn of 2004. Great Bustards were formerly widespread in England, and although many of the key areas have changed since the species became extinct, it was believed that Salisbury Plain, a Special Protection Area of calcareous grassland in South-West England bordered by agricultural areas, could provide a core area of suitable habitat (Osborne 2005). Many newly-released bustards disperse away from their release site in winter; those which survive their first winter return and incorporate the release area into their home range (Burnside et al. 2012).

Here, we investigate year-round habitat preferences of released bustards in South-West England and test for differences between sexes using Maximum Entropy modelling with the aim of providing an evidence-based approach to selecting future release sites.

METHODS

Study species and release methodology

Great Bustards, reared from eggs threatened by farming practices in Saratov, Russia, have been transported and released at a single site on Salisbury Plain, Wiltshire, UK, annually from 2004 to 2010; a second release site was established in 2011, with birds being released at
both locations. Salisbury Plain is the largest continuous area of calcareous grassland in north-west Europe; there is a low density of settlements and roads, with land-use comprising a mix of low-intensity grazing, arable farmland and an extensive military training area (380km$^2$, Burnside et al. 2012). The Salisbury Plain Site of Special Scientific Interest and Special Protection Area covers 197km$^2$ and is protected under domestic legislation and the EU Birds Directive (Osborne 2005).

We used data from re-sightings and satellite telemetry from 47 males and 52 females released from 2004 – 2010, totalling 5101 and 5698 records for individually-identified males and females respectively. Satellite transmitters (LC4TM platform transmitter terminals (Microwave Telemetry Inc., Columbia, USA)) recorded the locations of 19 of these individuals once a day at midnight or at 6-hour intervals (at 06:00, 12:00, 18:00 and 0:00). Re-sightings were recorded by project staff members driving a monitoring route approximately in a 2km radius around the release site, however due to the unpredictability of locating birds away from the release site, the project relies upon opportunistic re-sightings by members of the public to locate birds further afield. Due to this species’ large size, rarity in the UK, project publicity and the presence of easily identifiable patagial tags, there were regular reports (adults aged 1-3 years old were re-sighted at least once a month for nine months of the year), which were followed up by the project team. This dataset gave 726 and 749 novel presence locations for identified males and females respectively, which were recorded simply as presence within a 100m by 100m area, without reference to the frequency of occurrence. As individuals were all released from the same release site, presence data were spatially-biased, with 37.2% of all presence localities being recorded within a 2km radius of the release site, 43.5% recorded between 2km and 10km of the release site and 19.3% outside a 10km radius of the release site. To control for bias through release site selection and monitoring intensity, we used a reduced dataset based on proximity to release site, where
only data from outside a 2km radius were included (409 locations from 23 males; 431 from 27 females).

Environmental data

Environmental data on elevation, slope of land, land-use type, distance from roads, settlements, woodland and power lines were collected for South-West England (total study area = 13,001 km²). We used Ordnance Survey Land-Form Panorama DTM (1:50000) elevation data in ESRI ArcMap (v. 10.1) to create a slope raster dataset using the Spatial Analyst package. Habitat classes were obtained from Centre for Ecology & Hydrology Land Cover Map 2007 data (LCM2007), which is based on combined summer and winter habitat data from Landsat-TM5, IRS-LISS3, SPOT-4 and SPOT-5 sensors. The main habitat classes included in the LCM2007 data typically associated with Great Bustards in wild populations are arable and horticulture (including annual crops, perennial crops and freshly ploughed land), improved grassland (distinguished from semi-natural grasslands based on its higher productivity, lack of winter senescence and location and/or context), semi-natural grassland (in the field, semi-natural grassland is classified on botanical composition into neutral grassland, calcareous grassland or acid grassland), and rough grassland (a mix of areas of managed, low productivity grassland, plus some areas of semi-natural grassland, which could not be assigned to neutral, calcareous or acid grassland with confidence; see http://www.ceh.ac.uk/documents/LCM2007DatasetDocumentation.pdf for further details). Data on the location of roads, urban areas and woodland were taken from the Ordnance Survey Mastermap dataset (1:1250 – 1: 10000). Together with data from National Grid data on the location of power lines (400kV and 275kV), we used ESRI ArcGIS to create distance-
to-feature rasters. All environmental data rasters were cut to the same extent and re-sampled
to give a resolution of 35m by 35m.

**Modelling approach**

Species distribution models were created using Maximum Entropy modelling in MaxEnt (v. 3.3.3k), which has been shown to be robust with small sample sizes due to its regularization procedure (Baldwin 2009). We investigated differences in habitat preferences between sexes by creating separate sets of candidate models, and comparing the model-averaged estimates of variable importance between sets of models.

Models were run ten times, giving model averaged estimates, with default settings (regularization multiplier $\beta = 1$; number of background points = 10 000; convergence threshold = 0.00001) and background points were randomly selected from the whole of the study area. For each replicate, 25% of the data was randomly selected and removed without replacement for model evaluation. MaxEnt calculates presence probability based on sampling pixels where species are present, indicating the suitability of a given pixel relative to all other pixels; these raw probabilities are scaled to sum to 1 and do not represent probability of occurrence, but rather an index of relative suitability (Phillips *et al.* 2006). The area under the curve of a receiver operating characteristic (ROC) plot (AUC) was used as a threshold independent measure of accuracy (Swets 1988). AUC values range between 0 and 1, with maximum accuracy achieved with values of 1, accuracy no better than random with values of 0.5 and values <0.5 indicating performance worse than random. Using presence-only data, maximum AUC values should theoretically be less than 1, as AUC calculation is also dependent on absence data (Phillips *et al.* 2004). We assessed models by AUC accordingly: 0.5-0.6 = insufficient; 0.6-0.7 = poor; 0.7-0.8 = average; 0.8-0.9 = good; 0.9-1 = excellent (Hu *et al.* 2010). For each set of candidate models, percentage contribution of environmental
factors was averaged across the ten replicate models; the higher the contribution, the more
impact the environmental factor has on predicting the occurrence of the species.

As the quantity of presence data varied between individuals and MaxEnt does not allow the
estimation of the effect of individuals on the models, we removed data from individuals
contributing more than 10 presence data values from the full dataset, and compared the
models to the full single-sex models. Where individuals contributed less than 10 values, we
grouped them and ran the model removing this grouped data (individuals in grouped dataset:
Males = 10; Females = 16). These jack-knifed models were then compared to the full single-
sex models using AUC values to indicate model performance and Chi-square tests on the
average percentage contribution values for environmental variables to assess the impact of
removing individuals on the model predictions.

Response curves, showing how each environmental variable affects the MaxEnt prediction
were compared between male and female model sets. We classed preferred habitat as areas
with average predicted values greater than the average threshold of maximum training
sensitivity plus specificity over sets of ten replicate models to create predictive maps. We
then used The Map Comparison Kit (Visser & Nijs 2006) to compare maps of predicted
preferred area from male and female models using the map comparison kappa (MCK). MCK
quantifies the similarity between two maps on a scale from -1 (total dissimilarity), through 0
(no similarity) to 1 (identical maps) (Pontius 2000) and is based on the percentage of
agreement between two maps, corrected for the fraction of agreement that can expected by
chance (Visser & Nijs 2006).

RESULTS
Sex differences in habitat use

For males, the most important environmental variables were distance from roads and from settlements (Fig 1a). Distance from roads produced the largest gain, the improvement in penalized average log-likelihood compared to a null model, when used in isolation and also decreased the gain the most when it was omitted from the models, suggesting that it contained the most useful information by itself and also had the most information not present in other variables.

In contrast, for females the most important environmental variable was land-use type (Fig 1a). The variable with the highest gain when used in single-variable models was land-use, suggesting that this contained the most useful information on its own. However, the variable that decreased the gain the most when omitted from the female models was elevation, suggesting that this variable contained the most information not present in the other variables considered.

As land-use type differed in importance between the sexes, we further investigated which type of land-use may be responsible for the difference. Females and males were predicted to show similar preference levels for arable and horticulture (t-test: $t_{17} = 0.73$, $p = 0.5$), whereas females were predicted to prefer calcareous grassland four times more than males (Mean predicted preference: Females = $1.5 \pm 0.06$; Males = $0.38 \pm 0.04$; Wilcoxon rank sum test: $W = 100$, $p < 0.001$; Fig 1b). Both males and females were predicted to avoid improved grassland, with males more so than females (Mean predicted preference: Females = $-0.22 \pm 0.06$; Males = $-0.45 \pm 0.05$; Wilcoxon rank sum test: $W = 80$, $p < 0.005$). The sexes differed in their preference for rough low-productivity grassland, with males showing a positive preferences and females showing avoidance (Females: $= -0.6 \pm 0.11$; Males = $0.2 \pm 0.06$; t-test: $t = -7.9$, $p < 0.001$; Fig 1b).
Both sexes were predicted to have the highest probability of presence at low altitudes < 50m), above which probability of presence decreased; females, however, avoided high elevations more than did males (Fig 2a). For slope, both males and females were predicted highest presence at slopes less than 10 degrees (Fig 2b). Males and females showed a similar relationship to distance from power lines, with increasing predicted probability of occurrence from 0m, peaking around 500m, afterwards decreasing (Fig 2c). There was a greater probability of being closer to a power line within a 10-kilometre area around the release site than across the study area, suggesting that the observed decline in predicted preference at distances > 500m is due to the reduced availability of habitat further away from power lines local to the release site (based on values from 10,000 random pixels across the study area: Wilcoxon rank sum test: W = 4849255, p = 0.016).

Both sexes showed a positive relationship between predicted probability of presence and distance from roads; this relationship was stronger for males than females (Fig 2d). Also, a positive relationship was also found with distance from settlements (Fig 2e); however, here females showed a stronger relationship than males, but this variable was not found to contribute as significantly to models for females as for males, as discussed previously (Fig 1). Both sexes were also predicted to avoid wooded areas (Fig 2f).

To test the sensitivity of results to particular individuals, we deleted each individual and re-ran the models. The AUC scores were comparable and the models were still robust (Table 1). In only one model, where one particular male (P5) was removed providing 56.2% of all male novel presence data, were the percentage contributions of the environmental factors significantly different from the full single-sex model ($\chi^2 = 17.1$, p = 0.01). In the latter case, the ranks of the top four environmental variables were identical with the full model, only the
ranks of the variables of low importance were altered (Table 1), suggesting that the change was quantitative, but not qualitative.

**Predictive mapping**

Within the study area, 57.6% was predicted to be preferred for females, whereas only 37.9% was predicted to be preferred for males (Fig 3). The map comparison gave $\kappa = 0.37$, indicating low agreement between male and female preferred areas. Common preferred areas for males and females within the study constituted 17.7% (Fig 3).

Salisbury Plain Training Area was considered to provide the largest area of suitable habitat for Great Bustards in the UK by a feasibility study completed in 2003, and the current results are consistent with this view. Although the three ranges of the training area (East, Centre and West) did not differ in the proportion of different land-use types (GLM with quasi-binomial errors: $F_{2,26} = 0.0014, p > 0.5$), they did differ in the other environmental factors investigated. Land within the centre range was on average significantly further away from settlements and roads than land in the east and west ranges (Distance from settlements: Centre = 2.2 ± 0.05km; East = 1.1 ± 0.04; West = 1.4 ± 0.03; Kruskal-Wallis test: $K_{2,97649} = 20 335, p < 0.001$; Distance from roads: Centre = 2.0 ± 0.05km; East = 1.1 ± 0.05; West = 1.5 ± 0.04; Kruskal-Wallis test: $K_{2,97649} = 13 251, p < 0.001$). Also, the west range has greater elevation and slope on average compared to the centre and west ranges (Kruskal-Wallis test: Elevation: $K_{2,97649} = 12 860, p < 0.001$; Slope: $K_{2,97649} = 2586, p < 0.001$). These differences have resulted in a greater proportion of the centre and east ranges predicted to be preferred habitat than the west range (% preferred: Males: Centre = 74.2%; East = 49.8%; West = 18.0%; Females: Centre = 80.6%; East = 70.1%; West = 32.8%; Fig 3).
DISCUSSION

Habitat preference modelling is an important tool in conservation, and here we show sex-specific habitat preferences in released captive-reared Great Bustards in the UK. The results suggest that, although fragmented, there is sufficient preferred habitat within the UK to establish a viable population of this species. In addition, as these captive-reared individuals showed similar habitat preferences to individuals from wild populations, we suggest that there is an innate component to these preferences.

Sex-specific niche partitioning has been demonstrated in birds, mammals and reptiles (Mysterud 2000; Pearson et al. 2002), and here we show differential habitat preferences between sexes in a bird species with extreme sexual size-dimorphism. Males selected habitat based mainly on the distance from roads and settlements, whereas females selected habitat based mainly on land-use type. The largest difference between the sexes in their land-use preferences was the preference of females for calcareous grassland over arable and horticulture areas, whereas males were not found to show a preference; this may reflect differences in the diet and breeding habitat requirements between sexes (Moreira et al. 2004).

For example, in the breeding season females may prefer natural grassland areas as a result of greater cover provided while incubating and rearing chicks (Gray et al. 2009; Magaña et al. 2010). In addition, bustard chicks consume an invertebrate-rich diet to support their high growth rate, with around 30-35% of their diet consisting of invertebrates (Gewalt 1959; Bravo et al. 2012), compared to around 6% in adults (Lane et al. 1999; Rocha et al. 2005).

Lowland calcareous grassland areas in southern England are highly valued for their diverse plant and invertebrate communities (Mortimer et al. 1998), which may result in females choosing to be within or close to these areas when breeding. Breeding males, however, may show different preference from females due to the advantages of performing breeding.
displays in areas of shorter vegetation for maximum detectability of visual signals (Olea et al. 2010). However, males may choose to display in areas close to good breeding habitat or food resources that can potentially be used by females during their visit to the lek or when nesting and rearing chicks (Traba et al. 2007).

The key variables influencing Great Bustard distributions in the UK were distance from roads and settlements, and land-use type, consistent with wild populations studied elsewhere in Europe (Martínez, 1991; Lane et al. 2001; Osborne et al. 2001; Moreira et al. 2004). Great bustards are a shy species, vulnerable to human disturbance (Sastre et al. 2009), preferring habitat further away from human infrastructure. Although Great Bustards released in the project are captive-reared and not given training in suitable feeding or roosting sites, they show similar habitat preferences to individuals in wild populations (Lane et al. 2001; Osborne et al. 2001; Moreira et al. 2004), suggesting that habitat preferences may be innate. However, natal habitat preference induction or habitat imprinting theory (Immelmann 1975; Davis & Stamps 2004) suggests that free-living dispersers prefer habitats that contain stimuli comparable to those in their natal habitat; therefore releasing birds in an area considered by conservation managers to be suitable habitat for Great Bustards may cause preferences for habitat resembling their release site. Females typically return to their natal lek to breed (Alonso & Alonso 1992; Burnside et al. 2012), therefore by releasing birds at a particular site we may be effectively selecting the breeding areas of the founder population.

Furthermore, by releasing birds in a single location in southern England, we are potentially restricting the choices of habitat for released birds; although some habitats are preferred by the released birds does not necessarily indicate that they are optimal. Nevertheless, our results can be used to identify areas where there is a network of preferred habitat, highlighting areas where habitat management should be focussed and helping to inform the location of future release sites. Releasing individuals at multiple sites may produce higher population growth.
and greater spatial expansion than releasing individuals at a single site as it reduces intraspecific competition (Berger-Tal et al. 2012); therefore the consideration of new release areas may be critical to reintroduction success. Our results support early work identifying suitable areas for Great Bustards in the UK (Osborne 2005), and suggest that despite the movement of Great Bustards into more agricultural landscapes in other populations (Lane et al. 2001; Morales & Martín 2002), natural grassland is still an important habitat for this species. From our models, we found that overlapping areas of preferred habitat for males and females was nearly 18% in the study area; therefore habitat predicted to be preferred is not a limiting factor for Great Bustards in South-West England. Dispersal away from managed release areas can be detrimental to reintroduction projects, as individuals may become vulnerable to the threats that led to the previous extinction of the wild population (Le Gouar et al. 2012). In the Great Bustard reintroduction project, many individuals have dispersed away from the release areas in the autumn following release, which may be due to innate dispersal behaviours, social stimuli from conspecifics, or low suitability of habitat around the release site. If sub-optimal habitat is related to dispersal, selecting release sites based on the availability of preferred habitat or managing habitat specifically for bustards may help to reduce these movements (Martín et al. 2012).

In conclusion, we argue that for reintroduction projects, understanding habitat selection behaviour, and how this differs between life stages and sexes, is critical for designing targeted species-specific habitat management plans and the selection of release sites. Using Great Bustards, a species exhibiting one of the most extensive sexual size dimorphism among birds, we predict sexes differed in their habitat selection behaviour, having implications on conservation management for this species.
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Selection of breeding territory by little bustard (*Tetrax tetrax*) males in Central Spain:
Table 1. Comparison of Maximum Entropy models excluding data from single or grouped individuals with the full model (including data from all individuals). Sample sizes represent the total number of novel presence locations. Sample sizes used in models and removed sample sizes and the percentage of the full dataset removed shown. Model values shown are averaged across ten replicate models. Ranks of variable importance shown in brackets and Chi-square tests used to test for differences in the percentage contribution of environmental variables to models between the full model and the jack-knifed model.

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<th>Standard deviation</th>
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Figure 1. Contribution of variables to predicted occurrences of male and female Great Bustards: (a) environmental variables; (b) land-use categories. Values are averaged across 10 replicate models and error bars show ±1 S.E.

Figure 2. Relative predicted occurrence of Great Bustards predicted in relation to environmental variables, in relation to (a) elevation, (b) distance from power lines, (c) distance from public roads, (d) distance from settlements, (e) distance from woodland, and (f) slope. Females shown in red, males in black. Error bars represent ±1 S.E.

Figure 3. Predicted preferred area of male and female Great Bustards in South-West England. Average values from 10 replicate models are shown. Areas considered to be preferred if greater than the average threshold of maximum training sensitivity plus specificity. Pink, blue and green areas show the predicted preferred habitat for females, males and both sexes, respectively. White areas show area not predicted to be preferred habitat. Ministry of Defence Salisbury Plain Training Area shown as black hatched area, and major settlements shown in filled black areas. County boundaries bordered in black.
Figure 1. Contribution of variables to predicted occurrences of male and female Great Bustards: (a) environmental variables; (b) land-use categories. Values are averaged across 10 replicate models and error bars show ±1 S.E.
Figure 2. Relative predicted occurrence of Great Bustards predicted in relation to environmental variables, in relation to (a) elevation, (b) distance from power lines, (c) distance from public roads, (d) distance from settlements, (e) distance from woodland, and (f) slope. Females shown in red, males in black. Error bars represent ±1 S.E.

233x243mm (72 x 72 DPI)
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191x176mm (150 x 150 DPI)