



Response of young and adult birds to the same environmental variables and different spatial scales during post breeding period

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Abstract

Context How do young birds achieve spatial knowledge about the environment during the initial stages of their life? They may follow adults, so gaining social information and learning; alternatively, young birds may acquire knowledge of the environment themselves by experiencing habitat and landscape features. If learning is at least partially independent of adults then young birds should respond to landscape composition at finer spatial scale than adults, who possess knowledge over a larger area.

Objectives We studied the responses of juvenile, immature and adult Caspian Gull *Larus cachinnans* to the same habitat and landscape variables, but at several spatial scales (ranging from 2.5 to 15 km), during post-breeding period.

Methods We surveyed 61 fish ponds (foraging patches) in southern Poland and counted Caspian gulls.

Results Juvenile birds responded at finer spatial scales to the factors than did adults. Immature birds showed complicated, intermediate responses to spatial scale. The abundance of juvenile birds was mostly correlated with the landscape composition (positively with the cover of corridors and negatively with barriers). Adult abundance was positively related to foraging patch quality (fish stock), which clearly required previous spatial experience of the environment. The abundance of all age classes were moderately correlated with each other indicating that social behaviour may also contribute to the learning of the environment.

Conclusions This study shows that as birds mature, they respond differently to components of their environment at different spatial scales. This has considerable ecological consequences for their distribution across environments.

Keywords Age · Competition · Dispersal · Foraging · Landscape · Learning

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Introduction

Dispersal is a key process affecting the local population dynamics, patch occupancy and metapopulation functioning (Paradis et al. 1998). In birds dispersal is predominantly done by young individuals (Greenwood and Harvey 1976; Forero et al. 2002), with adult

birds usually showing strong level of philopatry to breeding sites (Lavers et al. 2007; Devlin et al. 2008). On the contrary, young birds differ in dispersal pattern, with natal dispersal distances typically considerably exceeding breeding dispersal (Paradis et al. 1998; Breton et al. 2006). Thus, these young birds play an important role in colonizing new breeding habitat patches, gene flow, population growth and dynamics, and range expansion (Breton et al. 2006; Lisnizer et al. 2015; Wey et al. 2015). Although juvenile dispersal has important consequences for population dynamics, the post-fledging period is perhaps the least studied and least understood part of the avian life cycle (Kershner et al. 2004). This period is critical for animals (Paradis et al. 1998, 1999): juveniles must cope with novel environments, compete with more experienced adults for resources and, as a probable consequence, usually have lower survival rates than adults (Greenwood and Harvey 1976). Typically, the most crucial problem for juvenile birds at this time is to find sufficient food resources so as to survive over the winter (Szostek and Becker 2015).

Landscape structure influences the spatial movement of organisms as they often affect dispersal ability and behaviour (van Dyck and Baguette 2005). Landscape structure may enhance, or hinder, movements between foraging habitat patches (Beier and Noss 1998; Skorka et al. 2009), which may influence the survival rate of individuals (Harris and Reed 2002).

Thus, how can young birds gain information about novel environments? Firstly, they may follow adults in copying their behavior and foraging site choice (Lefebvre 1986; Slagsvold and Wiebe 2011). However, the social learning may possess substantial costs for young birds. They are usually subordinate to adults and less-efficient foragers; thus, when in a foraging habitat patch, they may suffer from lower food intake due to competition, kleptoparasitism, aggression or food depletion (Gochfeld and Burger 1981; Carroll and Cramer 1985; Skorka and Wojcik 2008). The drawback of the competitive advantage of adults disappears if young birds seek food patches unoccupied by adults. This is certainly challenging since young birds are unfamiliar with the environment outside the natal territory/colony. However, they may use landscape features that lead them to foraging patches, and consequently to brain mapping and learning of the environment (Bird et al. 2003; Healy and Hurly 2004).

It is currently unknown how different age individuals perceive landscape features and how this affects aggregation. Learning and acquiring information is obviously time dependent; thus one may hypothesize that unfamiliarity with the environment implies that young birds will respond to landscape elements at a finer scale when finding foraging patches. In contrast, older individuals may use their prior knowledge and exploit already known high-quality foraging patches (Klaassen et al. 2007). Also, adults may use information from a wider area explored earlier and, thus, respond to landscape features at larger spatial scales. Thus, while both adults and juveniles should use clues that will help them discover foraging patches, juveniles should use and respond to larger number of landscape elements at finer spatial scale than adults. However, an opposite scenario is also possible. In birds natal dispersal is characterized by longer movement than breeding dispersal performed by adults (Kilpi and Saurola 1983; Paradis et al. 1998, 1999). Therefore, if juvenile birds interact with many landscapes during natal dispersal, they may possibly respond to factors acting at larger spatial scales than adult birds.

The aim of this study was to investigate how Caspian gull *Larus cachinnans* of different age classes respond to the same environmental factors, some of them measured at up to six spatial scales during the post breeding period. We focused on factors affecting the abundance of birds in foraging patches as finding food is a key factor determining survival rates during the post-breeding period. We tested five predictions:

- (1) The abundance of birds from all age classes in foraging habitat patches is positively related to the density of movement corridors, but juveniles should respond to these structures at smaller spatial scales if they learn independently of older birds.
- (2) Movement barriers should negatively affect abundance of birds in foraging patches, while juvenile birds should respond to them at lower spatial scales than adults.
- (3) Adult birds possess prior information about the landscape; thus their abundance should be positively affected mostly by density of food resources in the foraging habitat patches (e.g. fish stock, fish size).
- (4) Learning about the environment involves interactions with numerous patch and landscape

characteristics, so the abundance of juvenile birds should be determined by more factors than for older birds.

- (5) If social interactions play a role in acquiring knowledge of the environment, a positive correlation is expected between abundances of juvenile and older birds in foraging habitat patches.

Materials and methods

Study species

The Caspian gull is a colonial species that inhabits waterbodies, whose native range extends from the Black Sea eastwards through the steppe zones, reaching eastern Kazakhstan (Malling Olsen and Larsson 2004). Since the 1980s the Caspian gull population has grown rapidly and expanded north and west, mainly along large river valleys (Filchagov 1996; Jonsson 1998) due to the availability of trawler discards from fishing boats, domestic refuse and a high breeding success in newly colonized areas (Skorka et al. 2005; Lenda et al. 2010). Caspian gulls breed on islets or shores of inland waterbodies in colonies comprising up to a few hundred breeding pairs. The breeding season extends from the end of March to the beginning of June. Juvenile birds stay at the colony until the middle of July, then disperse.

Their diet mostly comprises fresh fish, mainly carp *Cyprinus carpio* obtained from fish ponds (Skorka et al. 2005; Gwiazda 2004; Gwiazda et al. 2011, 2015). The proportion of carp in the diet was 70 % of all items in breeding season, but lower outside this period (Skorka et al. 2005; Gwiazda et al. 2011). The gulls captured fish varying between 5 and 47 cm (Gwiazda 2004; Gwiazda et al. 2011, Skórka unpublished). The size of fish captured does not differ between adult, immature and juvenile birds (Skorka and Wojcik 2008).

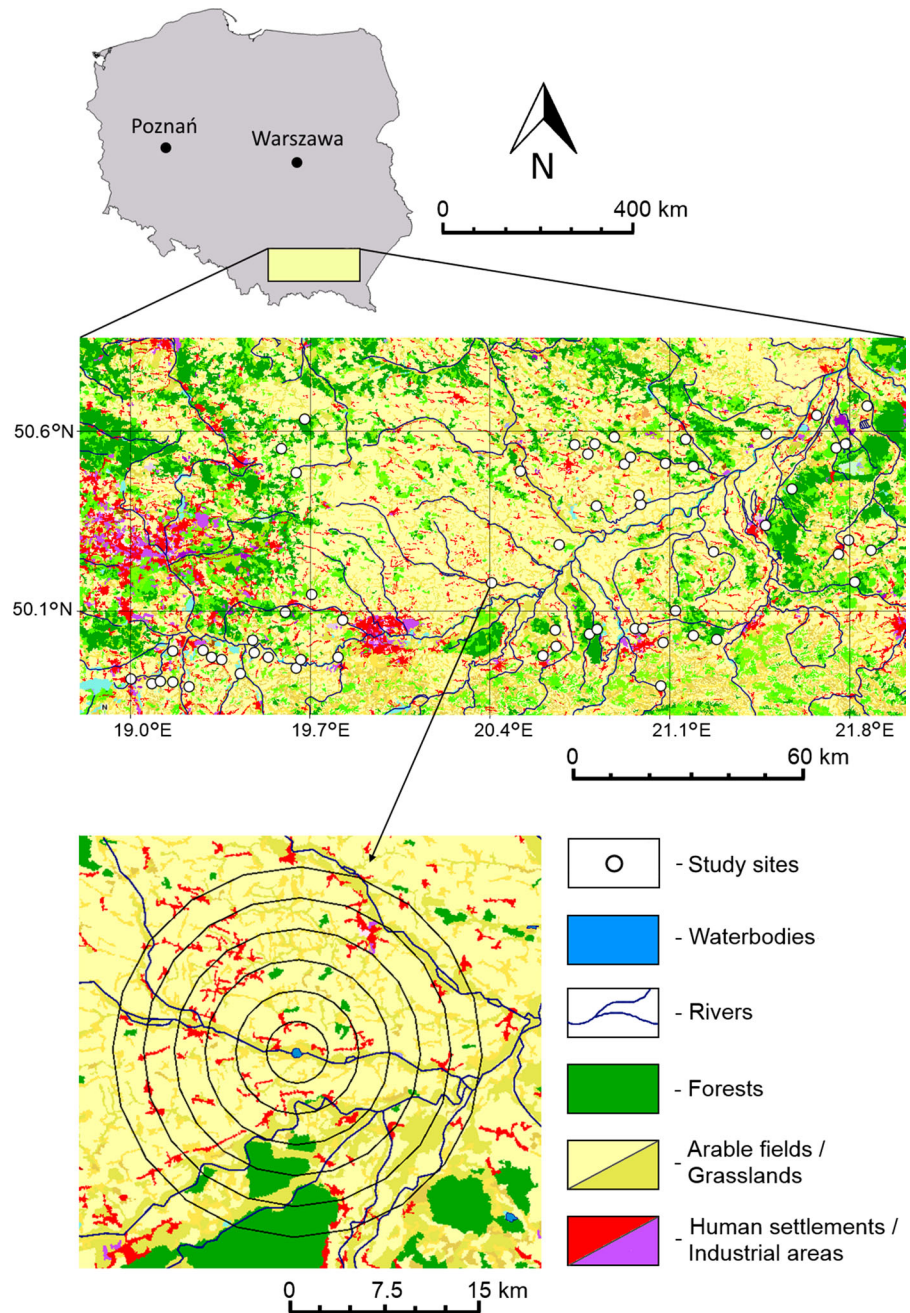
The plumages of juveniles, immatures and adults differ substantially, making aging straightforward. Juveniles are defined here as all birds in their first summer plumage (Jonsson 1998). This plumage is mostly white on the head neck and breast, largely grey on the back (with mantle feathers and scapulars having dark shafts), brown and white on the wing coverts, and dark black-brown on the primaries. Immature birds

were classified as individuals in their second or third summer or winter plumage (Jonsson 1998). These birds have mantle feathers largely plain grey, although some first-winter feathers with dark streaks remain. Some coverts are replaced with grey. The belly and breast sides are whiter, although the face retains some grey smudging around the eye. Second-winter birds frequently develop a faint white mirror in the longest primary. The bill base is pale to grey-flesh colour with a dark tip (Jonsson 1998). Adult birds have a grey back, black wing tips and yellow eye with many dark spots.

Field surveys

We conducted this study in south-eastern Poland (Fig. 1). Dominant land use cover is open agricultural land (70 % land cover) while forest covers 16 % and human settlements 12 % (Fig. 1; Table 1). Water bodies in this region are patchily distributed and cover about 2 % of land (Fig. 1). We randomly choose 61 fish farms, referred to as ‘foraging habitat patches’. The selection was achieved by generating random coordinates and taking the nearest fish pond complex. Ponds separated by less than 50 m were treated as one habitat patch as such ponds are typically just separated by 20–50 m embankments, and used by gulls as a single habitat patch (Skorka et al. 2009). Each study pond was visited twice between 15th August and 15th September 2011. Mean \pm SE time between two surveys was 15 ± 0.1 days (range: 14–17 days). Surveys were conducted during good weather conditions, without rain and wind speed up to 4° in the Beaufort scale (see: Supplementary Electronic material). Three experienced persons took part in observations. During one visit an observer usually counted birds in 4–6 ponds. Thus, with three persons involved between 12 and 15 ponds could be visited in 1 day. It took 5 days in total to complete first survey and 6 days to complete the second one. In larger fish-farms (>100 ha) birds were counted with help of other experienced observers from two or three stations covering different parts of the farm. We behaved in a way to minimize our impact on bird behaviour. Observations were performed from the border of fish ponds with the use of $\times 10$ binoculars. We did not see any sign of adverse behaviour in birds (escape, frightening) in appearance of observers. We also did not observe negative reaction of these gulls to workers feeding fishes or performing some

Fig. 1 The map (Corine land cover: <http://www.eea.europa.eu/data-and-maps>) of study region located in the south-eastern Poland (*upper panel*). The location of each of the 61 fish-farms is shown by white dots. An example of one study site with a surrounding landscape is in lower panel (*lower panel*). Radii of 2.5, 5, 7.5, 10, 2.5, 15 km that were used in the landscape analyses are shown by ellipses



maintenance works. The abundance of birds during two surveys was strongly correlated suggesting constancy in habitat patch use in the study period (Fig S1 in Electronic Supplementary Material). Each patch was observed for 5 min and the number of Caspian gulls of each age class noted between 6:00 and 11:00.

During this part of a day Caspian Gulls forage intensively. The foraging gulls either fly above the water surface or swim in the open. Thus, our observations mostly encompassed gulls that foraged in habitat patches. The 5 min time span was sufficient to detect all individuals, as Caspian gulls are large

Table 1 Basic characteristics (mean, standard deviation, minimum and maximum values) of the investigated variables

Variable	Variable code	Mean	SD	Min.	Max.
Maximal abundance of juvenile Caspian gulls	Juvenile	8.30	9.13	0.00	34.00
Maximal abundance of immature Caspian gulls	Immature	3.30	4.25	0.00	22.00
Maximal abundance of adult Caspian gulls	Adult	5.72	5.76	0.00	20.00
Foraging patch area [ha]	Area	60.68	102.19	1.00	661.50
Distance to the nearest breeding colony [km]	Nearest colony	19.02	14.16	0.84	54.57
Fish stock [$\text{kg} \times \text{ha}^{-1}$]	Fish density	879.38	756.85	41.97	3834.89
Mean fish size in pond [cm]	Fish size	24.5	2.4	20.1	28.5
Cover [%] of waters in a 2.5 km radius	Water (2.5 km)	0.03	0.04	0.00	0.16
Cover [%] of waters in a 5 km radius	Water (5 km)	0.02	0.02	0.00	0.09
Cover [%] of waters in a 7.5 km radius	Water (7.5 km)	0.02	0.02	0.00	0.08
Cover [%] of waters in a 10 km radius	Water (10 km)	0.02	0.02	0.00	0.08
Cover [%] of waters in a 12.5 km radius	Water (12.5 km)	0.01	0.01	0.00	0.06
Cover [%] of waters in a 15 km radius	Water (15 km)	0.01	0.01	0.00	0.05
Cover [%] of forests in a 2.5 km radius	Forest (2.5 km)	0.17	0.17	0.00	0.91
Cover [%] of forests in a 5 km radius	Forest (5 km)	0.17	0.13	0.00	0.57
Cover [%] of forests in a 7.5 km radius	Forest (7.5 km)	0.15	0.09	0.01	0.39
Cover [%] of forests in a 10 km radius	Forest (10 km)	0.16	0.08	0.03	0.36
Cover [%] of forests in a 12.5 km radius	Forest (12.5 km)	0.16	0.07	0.03	0.31
Cover [%] of forests in a 15 km radius	Forest (15 km)	0.17	0.08	0.01	0.39
Density of rivers [$\text{km} \times (\text{km}^2)^{-1}$] in a 2.5 km radius	River (2.5 km)	0.14	0.12	0.00	0.38
Density of rivers [$\text{km} \times (\text{km}^2)^{-1}$] in a 5 km radius	River (5 km)	0.13	0.08	0.00	0.31
Density of rivers [$\text{km} \times (\text{km}^2)^{-1}$] in a 7.5 km radius	River (7.5 km)	0.12	0.06	0.00	0.30
Density of rivers [$\text{km} \times (\text{km}^2)^{-1}$] in a 10 km radius	River (10 km)	0.13	0.06	0.00	0.31
Density of rivers [$\text{km} \times (\text{km}^2)^{-1}$] in a 12.5 km radius	River (12.5 km)	0.13	0.06	0.00	0.27
Density of rivers [$\text{km} \times (\text{km}^2)^{-1}$] in a 15 km radius	River (15 km)	0.13	0.06	0.00	0.26
Cover [%] of settlements in a 2.5 km radius	Settlement (2.5 km)	12.41	6.50	4.31	30.22
Cover [%] of settlements in a 5 km radius	Settlement (5 km)	12.25	5.55	6.52	30.29
Cover [%] of settlements in a 7.5 km radius	Settlement (10 km)	11.88	4.57	7.29	30.22
Cover [%] of settlements in a 10 km radius	Settlement (7.5 km)	12.11	4.99	7.02	29.37
Cover [%] of settlements in a 12.5 km radius	Settlement (12.5 km)	11.99	4.49	7.44	29.37
Cover [%] of settlements in a 15 km radius	Settlement (15 km)	12.07	4.39	7.42	28.02

birds (56–68 cm long, with a 140–150 cm wingspan and a body mass of 700–1600 g; Malling Olsen and Larsson 2004). The locations from which birds were counted enabled a sufficient view of either the entire reservoir or the part assigned to a particular observer. Therefore, we believe that all birds present in each foraging patch were counted. We selected this short observation time also to avoid possible double counting—during longer observations at larger patches more birds could have been counted at least twice as these gulls frequently move within habitat patches (Skorka et al. 2009).

Environmental variables

For each patch, we noted following variables: (1) area (ha), (2) fish stock (kg/ha), (3) mean fish size (cm), (4) distance (km) to the nearest breeding colony, (5) area of human settlements in surrounding landscape, (6) forest area in surroundings, (7) waterbodies in the surrounding landscape and (8) river density (km per 10 km^2) in the surrounding landscape. Variable (3), the mean fish size, was estimated from fish farm data on stock, common carp age class frequency and body mass of each age class. Young-of-the-year carp

reaches 10 cm in August and weigh about 20 g, 1-year-old carps are about 25 cm and weight 250 g, and 2-year-old carps reach 30 cm and 1 kg (Mazurkiewicz 2009). Fish exceeding 3 years were assumed to reach 40 cm and 1500 g. Older carp are rarely being found in fish farms as production cycle is about 2 or 3 years (Dobrowolski 1995). Variables 5–8 were measured at six spatial scales: 2.5, 5, 7.5, 10, 12.5 and 15 km radii from the edge of foraging patch (ellipses in lower panel of Fig. 1). These scales encompasses the usual foraging movement of adult Caspian Gulls (Skorka et al. 2009); larger radii would have led to substantial spatial overlap of polygons. We used Corine Land raster database (available from: <http://www.eea.europa.eu/data-and-maps>) and Geoportal (WMS layer available from: <http://mapy.geoportal.gov.pl/imap/>) to acquire characteristics of variables 1 and 5–8. All measurements were done in QGIS 1.7. Wrocław geographical information system.

Statistics

Data analysis

Abundance data was analyzed for 61 selected study patches. We used maximum abundance recorded from two surveys. Maximum numbers were strongly correlated with mean ($r = 0.993$, $P < 0.001$) and minimal ($r = 0.960$, $P < 0.001$) numbers. There was no difference in mean abundance of birds from different age classes between two surveys (Electronic Supplementary Material). However, maximum abundance better characterized maximum habitat patch capacity and was selected due to the use of statistical models requiring integer numbers rather than real ones (when mean is calculated). Before building statistical models we checked if spatial autocorrelation needed to be incorporated in the analysis. However, Moran's I correlograms revealed no spatial correlation in the abundance of birds of any age class, thus we used ordinary generalized linear models (GLM) in analyses.

We started statistical analyses with single factor models testing the response of birds to landscape characteristics (cover of waters, forest, human settlements and density of rivers) at six spatial scales. GLM with Poisson error variance and log-link function was

fitted to the abundance of each age class and spatial scale. We used the corrected Akaike information criterion (AICc) to select the spatial scale, for a given environmental factor, that best predicts the abundance of birds for the three age classes (Bradter et al. 2013). We assumed that abundance of birds respond differentially to the spatial scales if ΔAICc differ more than two among scales (Burnham and Anderson 2002). The scale with the lowest AICc was then taken as that abundance of bird from a given age class is best predicted.

Having identified the spatial scale for landscape features that predicts the best abundance of birds we built multivariate GLM to test which environmental variables are the most important predictors of abundance of birds from each age classes. We used model selection based on AICc to find the subset of models that best explain the data. We built all model combinations and used models with ΔAICc below 2 as the best in predicting gull abundance (Burnham and Anderson 2002). We used model averaging (using set of models with ΔAICc below 2) to achieve estimates of function slopes. We used natural square root (covers of water, forest, distance to the nearest colony, fish density) or \log_{10} (cover of human settlement, patch area) transformation to reduce the effects of outlier observations and meet the assumption of homoscedasticity (Quinn and Keough 2002). In all regression models, variables were standardized (mean = 0 and standard deviation = 1) to allow for a direct comparison of estimates of function slopes.

In addition to multivariate GLMs, we also performed hierarchical partitioning (Chevan and Sutherland 1991) to determine the independent contribution of the explanatory variables on the abundance of each age classes. Hierarchical partitioning was performed using the 'hier.part' package version 1.0–3 (Walsh and Mac Nally 2015), which was implemented using the R statistical package version 3.1.1 (R Development Core Team 2004). Poisson distribution and log-likelihood were used as goodness-of-fit measures in the analyses. Hierarchical partitioning computes the increased fit for all models containing a given variable, compared to an equivalent model without that variable. The average improvement in fit (reduction in deviance) across all possible models containing that predictor is then computed. This process results in the estimation of the independent contribution of each explanatory

variable (I), and the joint contribution (J) resulting from correlation with other variables (Mac Nally 2000, 2002) so allowing the relative independent contribution of each predictor (% I) to be determined. A predictor with the percentage of I exceeding $100/K$ (where K is the number of predictors) was considered to have high explanatory power (Mac Nally 2000, 2002). Randomization tests that yield z -scores were used to determine statistical significance of the relative independent contributions based on an upper confidence limit of 0.95 (Mac Nally 2002). If results from model averaging and hierarchical partitioning differed then we used the latter method as conclusive.

Results

Predicting abundance of different age classes to six spatial scales

Total number of birds recorded was 506 juveniles, 201 immatures and 349 adults (Table 1). Mean number of juvenile, immature and adult gulls during one survey per fish pond was 7.0 ± 0.7 , 2.5 ± 0.3 and 4.8 ± 0.5 , respectively. The numerical response of juvenile birds to environmental factors differed across six spatial scales. The abundance of juvenile age class was the best predicted by variables measured at the scale 2.5 km (covers of water and settlements, density of rivers). Abundance of juvenile responded to forest cover measured at the scale of 10 km, however, the abundance was equally well predicted by forest cover measured at the 2.5 km scale (Fig. 2). All predictors of abundance were statistically significant (all $P < 0.05$) at the best predicting scale.

Abundance of immature birds was best predicted by variables acting at the scale of 7.5 km (water cover), 12.5 km (forest cover and settlement cover), 15 km (river density) (Fig. 2). The response to settlement cover was statistically non-significant at any scale (all $P > 0.05$, Fig. 2k).

Abundance of adult birds was the best predicted by variables acting at the scale of 2.5 km (settlement cover), 10 km (river density), 12.5 km (water cover) and 15 km (forest cover) (Fig. 2); the effect of human settlement cover on abundance of adults was not statistically significant at any scale (all $P > 0.05$, Fig. 2l).

Factors affecting abundance of birds from different age classes in foraging habitat patches

Juvenile birds

Four models best predicted abundance of juvenile birds in foraging habitat patches (Table 2): abundance was positively correlated with cover of water at the scale of 2.5 km, abundance of adults, and river density in 2.5 km radius, while abundance was negatively correlated with cover of human settlements in the 2.5 km radius and distance to the nearest breeding colony (Table 3). The best models also included effects of fish density and size, and abundance of immature birds (Table 2), however these variables were statistically non-significant (Table 3). Hierarchical partitioning revealed that among variables included in the best models the most important independent variables were water cover in the 2.5 km radius, abundance of adults, river density in 2.5 km radius and distance to the nearest colony (Fig. 3). Independent individual impact of settlement cover in 2.5 km radius, fish density, fish size and abundance of immature birds were all statistically non-significant (Fig. 3).

Immature birds

Eight models best predicted abundance of immature birds in foraging habitat patches (Table 2). The abundance was positively correlated with adult abundance, distance to the nearest breeding colony and cover of settlements in a 12.5 km radius (Table 3). The abundance was negatively correlated to the density of rivers in 15 km radius and cover of forest in 12.5 km radius (Table 2). The best models also included effects of patch area, abundance of juvenile birds, water cover in 7.5 km radius and fish size (Table 2), however these variables were statistically non-significant as indicated by model averaging (Table 3). Hierarchical partitioning revealed that among variables included in the best models the most important variables with statistically significant independent contribution were adult abundance, forest cover in a 12.5 km radius, water cover in the 7.5 km radius, river density in a 15 km radius and distance to the nearest colony (Fig. 3).

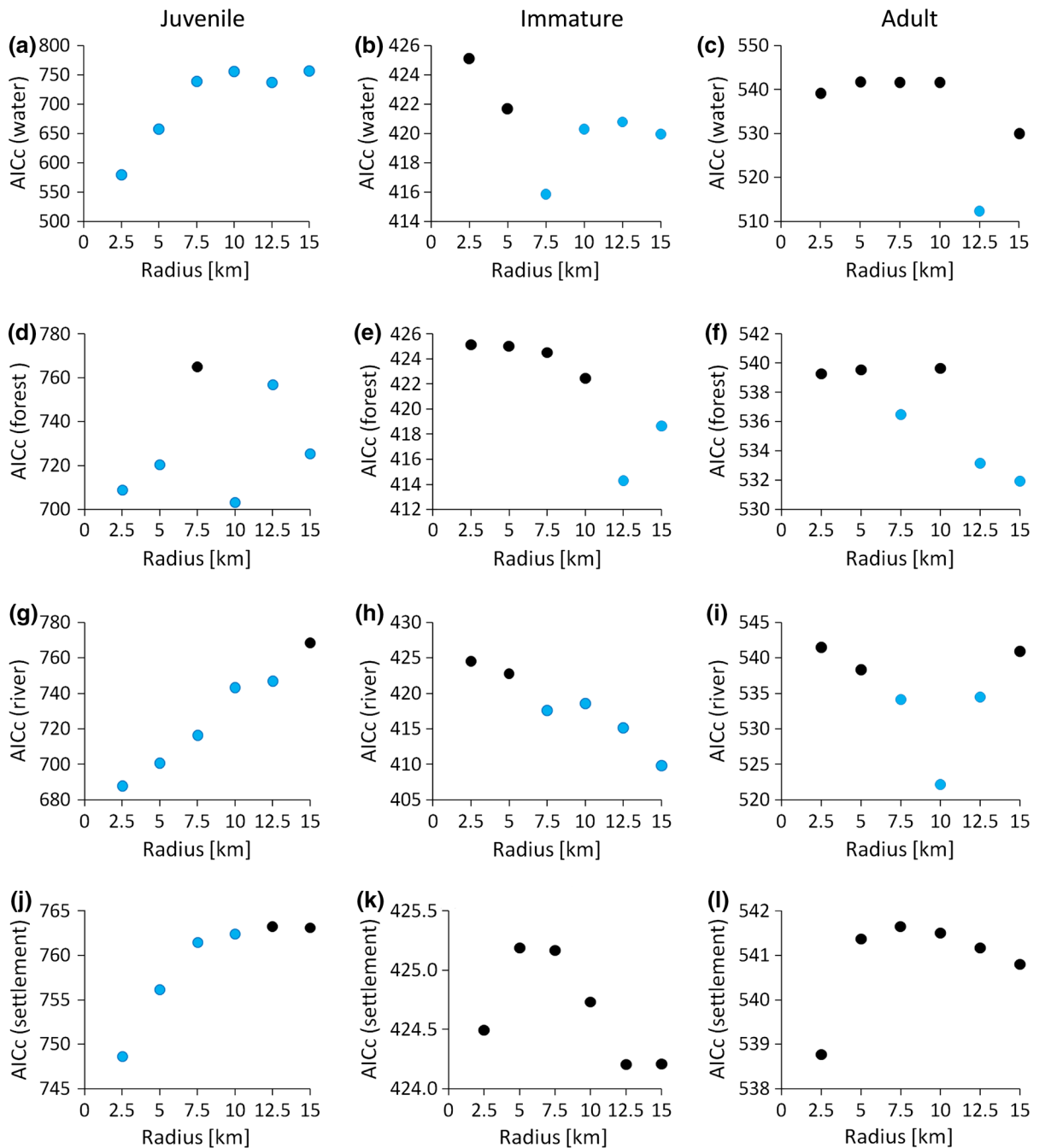


Fig. 2 Numerical response (*abundance*) of different age classes of Caspian Gull to different landscape features measured at six spatial scales. The statistically significant response of the abundance to a given scale is in blue (*bright*). The response of

juvenile, immature and adult Caspian gulls is in the *left* (a, d, g, j), in the *middle* (b, e, h, k) and in the *right panel* (c, f, i, l), respectively. (Color figure online)

Independent individual impact of settlement cover in 12.5 km radius, patch area, fish size and abundance of juveniles birds were all statistically non-significant (Fig. 3).

Adult birds

The three best models predicted abundance of adult birds in foraging habitat patches (Table 2). The

Table 2 Best generalized linear models describing abundance of juvenile, immature and adult Caspian Gulls in foraging patches during post breeding period

Model	df	logLik	AICc	ΔAICc	w
Juvenile					
Nearest colony + river (2.5 km) + settlement (2.5 km) + adult + water (2.5 km)	6	-243.64	500.83	0	0.23
Fish size + nearest colony + river (2.5 km) + settlement (2.5 km) + adult + water (2.5 km)	7	-242.16	501.34	0.51	0.18
Fish density + nearest colony + river (2.5 km) + settlement (2.5 km) + adult + water (2.5 km)	7	-243.16	502.44	1.61	0.11
Nearest colony + river (2.5 km) + settlement (2.5 km) + adult + immature + water (2.5 km)	7	-243.29	502.7	1.87	0.09
Immature					
Forest (12.5 km) + nearest colony + rivers (15 km) + settlement (12.5 km) + adults	6	-159.92	333.4	0	0.14
Area + forest (12.5 km) + nearest colony + rivers (15 km) + settlement (12.5 km) + adults	7	-158.77	333.64	0.24	0.12
Area + forest (12.5 km) + nearest colony + rivers (15 km) + settlement (12.5 km) + adults + juvenile	8	-157.81	334.39	0.99	0.11
Area + fish size + forest (12.5 km) + nearest colony + rivers (15 km) + settlement (12.5 km) + adults	8	-157.91	334.59	1.19	0.09
Fish size + forest (12.5 km) + nearest colony + rivers (15 km) + settlement (12.5 km) + adults	7	-159.26	334.62	1.22	0.06
Area + forest (12.5 km) + nearest colony + rivers (15 km) + settlement (12.5 km) + adults + water (7.5 km)	8	-157.93	334.62	1.22	0.06
Forest (12.5 km) + nearest colony + rivers (15 km) + settlement (12.5 km) + adults + juvenile	7	-159.49	335.1	1.7	0.05
Area + fish size + forest (12.5 km) + nearest colony + rivers (15 km) + settlement (12.5 km) + adults + juveniles	9	-156.82	335.18	1.8	0.05
Adult					
Area + fish density + river (10 km) + settlement (2.5 km) + immature + juvenile	7	-180.02	376.15	0	0.28
Area + fish density + river (10 km) + settlement (2.5 km) + immature + juvenile + water (12.5 km)	8	-179.52	377.81	1.66	0.12
Fish density + river (10 km) + immature + juvenile + water (12.5 km)	6	-182.21	377.97	1.82	0.11

The Akaike information criterion score (AICc), the log-likelihood (logLik), the difference between the given model and the most parsimonious model (Δ) and the Akaike weight (w) are listed. Explanation of variable codes are in Table 1

Table 3 Averaged estimates of the function slopes of variables present in the most parsimonious GLMs describing the abundance of juvenile, immature and adult Caspian Gulls in foraging habitat patches during post-breeding dispersal

Effect	Estimate	AdjSE	Z	P
Juvenile				
Intercept ^a	1.831	0.058	31.632	<0.001
Nearest colony	−0.137	0.051	2.707	0.007
River (2.5 km)	0.159	0.059	2.689	0.007
Settlement (2.5 km)	−0.245	0.054	4.571	<0.001
Adult	0.386	0.059	6.552	<0.001
Water (2.5 km)	0.429	0.057	7.470	<0.001
Fish size	−0.062	0.044	1.410	0.159
Fish density	−0.055	0.060	0.925	0.355
Immature	−0.046	0.054	0.849	0.396
Immature				
Intercept	0.919	0.092	9.985	<0.001
Forest (12.5 km)	−0.210	0.085	2.462	0.014
Nearest colony	0.381	0.095	4.023	<0.001
River (15 km)	−0.335	0.087	3.848	<0.001
Settlement (12.5 km)	0.204	0.083	2.468	0.014
Adult	0.496	0.099	5.010	<0.001
Area	0.181	0.113	1.610	0.107
Juvenile	−0.107	0.093	1.151	0.250
Fish size	−0.099	0.081	1.227	0.220
Water (7.5 km)	−0.141	0.135	1.042	0.298
Adult				
Intercept	1.492	0.068	21.800	<0.001
Area	0.175	0.085	2.058	0.040
Fish density	0.345	0.057	6.007	<0.001
River (10 km)	0.181	0.061	2.939	0.003
Settlement (2.5 km)	0.140	0.069	2.037	0.042
Immature	0.348	0.061	5.720	<0.001
Juvenile	0.279	0.073	3.824	<0.001
Water (12.5 km)	0.111	0.073	1.521	0.128

Statistically significant effects are given in bold

Adjusted standard errors (SE) are presented. Tests of significance of variables are given in the final two columns

^a A constant which is the expected mean value of dependent variable when all independent variables equal zero

abundance was positively correlated with abundances of immature and juvenile birds, fish density (Fig. 4), patch area, density of rivers in a 10 km radius and human settlements in 2.5 km radius (Table 3). The best models also included effects of water cover in 12.5 km radius (Table 2), however this variable was statistically non-significant (Table 3). Hierarchical

partitioning revealed that among variables included in the best models the most important variables with statistically significant independent contribution were fish density, the abundance of immature and juvenile birds, water cover in the 12.5 km radius and river density in a 10 km radius (Fig. 3). Independent individual impact of settlement cover in 12.5 km radius and patch area were statistically non-significant (Fig. 3).

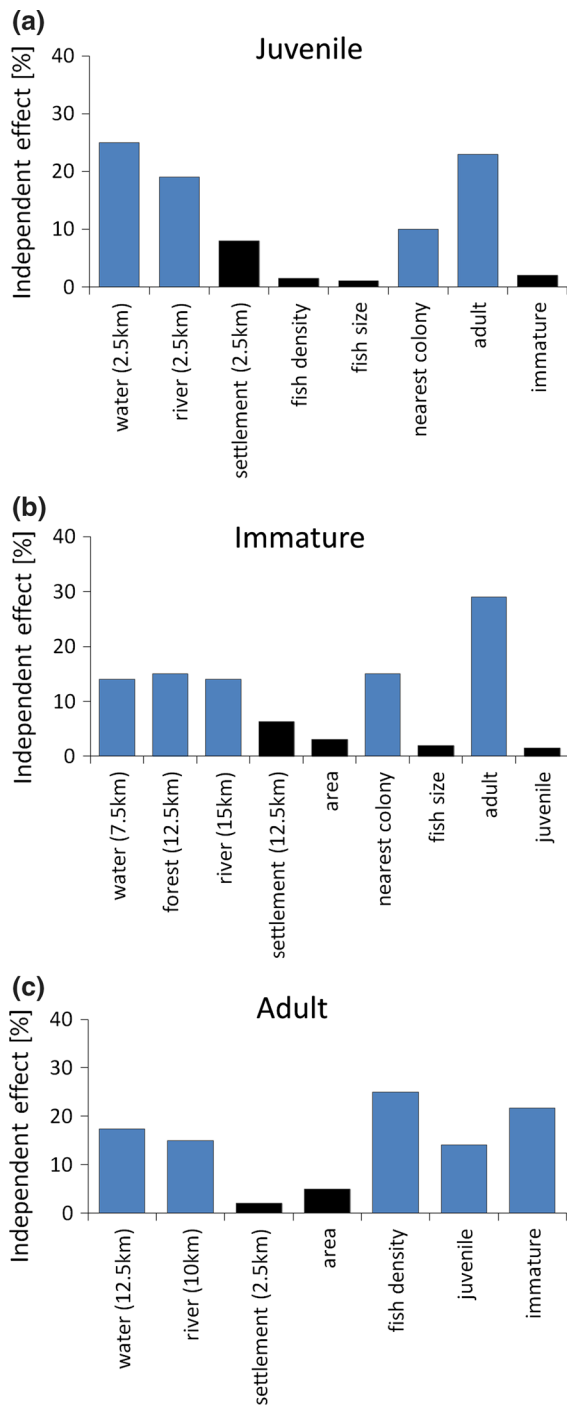
Landscape composition predictability across scales

For different landscape features, spatial scales were positively correlated between each other. However, the level of correlation between scales decreased with distance: neighbouring spatial scales were more positively correlated than distant ones (Fig. S2 in Supplementary Material). The most predictable landscape feature across spatial scales (positive correlation) was human settlement cover (Fig. S2 in Supplementary Material).

Discussion

Understanding habitat requirements at various life stages is important to predict population functioning and dynamics. Habitat-use patterns are influenced by ecological processes occurring at multiple spatial scales and several studies already focused on finding the most appropriate scale to measure (Beasley et al. 2007; Bradter et al. 2013). In this study we demonstrated that spatial scale is not only matter of methodology, but also has a profound biological meaning. We have shown, to the best our knowledge, for the first time that juvenile Caspian gulls differentially responded to spatial scales (for the same environmental factors) than older gulls during post-breeding period in the study region.

Abundance of juvenile birds was affected by landscape structure measured at smaller spatial scales than older birds. At the time of the study juvenile birds were about 3 month-old. They certainly were not familiar with the landscape or dispersed food resources. They were still attached to locations near breeding colonies indicating that natal site affect movements through landscape. This suggests that young birds gradually extend foraging patches away



from their natal colony. Juvenile gull abundance was strongly positively affected by movement corridors. Both water cover and river density positively correlated with their abundance. Blums et al. (2003) and Skorka et al. (2009) demonstrated that rivers and water

Fig. 3 Decomposition of the total reduction in deviance associated with environmental variables into independent components using the hierarchical partitioning method. The independent contribution of variables to abundance of juvenile (a), immature (b) and adult (c) Caspian gull. Variables that had the strongest and statistically significant ($P < 0.05$) impact on abundance of age classes are given in blue (bright bars). Only variables selected in the best models were included in this analysis

bodies play important role in landscape scale movements of waterbirds and their use of foraging patches. It is noteworthy that rivers also increase abundance in breeding habitat patches, as shown by Lenda et al. (2010). The importance of rivers as corridors perhaps results from the possibility of foraging during movement (Skorka et al. 2009). Our study also indicates that cover of human settlements may negatively affect juvenile gull abundance. The effect of this variable is, however, unclear. It was statistically significant in the best models; however hierarchical partitioning suggested its impact was not important. The possible negative effect of human settlement cover on abundance of juvenile gulls in fishpond may result from two phenomena. First, in larger settlements gulls may use refuse-tips as foraging habitat. Caspian gulls, however, gather at refuse tips in larger numbers only in late autumn and winter (Skorka and Wojcik 2008). The second possibility is that humans have direct negative effect on abundance, for example in waterbodies surrounded by dense settlements more people visiting/walking/fishing may disturb foraging birds (Fernández-Juricic and Tellería 2000). Moreover, we never observed this species foraging directly in human settlements (e.g. in litter bins, or in lawns) in the study area. Caspian gulls enter human settlements (e.g. towns) in winter but only if settlements are located along rivers and birds are attached to water bodies and rivers there (authors' unpublished data).

The abundance of immature birds was best predicted by variables at larger spatial scales than for juvenile birds. The relationship between abundance and environmental variables was more complicated than in juvenile and adult birds. Immature Caspian gulls encompass one-, two- and three-year old birds that certainly differ in experience and perception of the landscape. It is possible that some of these birds respond in a way similar to juveniles, while others respond in more similar manner to adults so generating

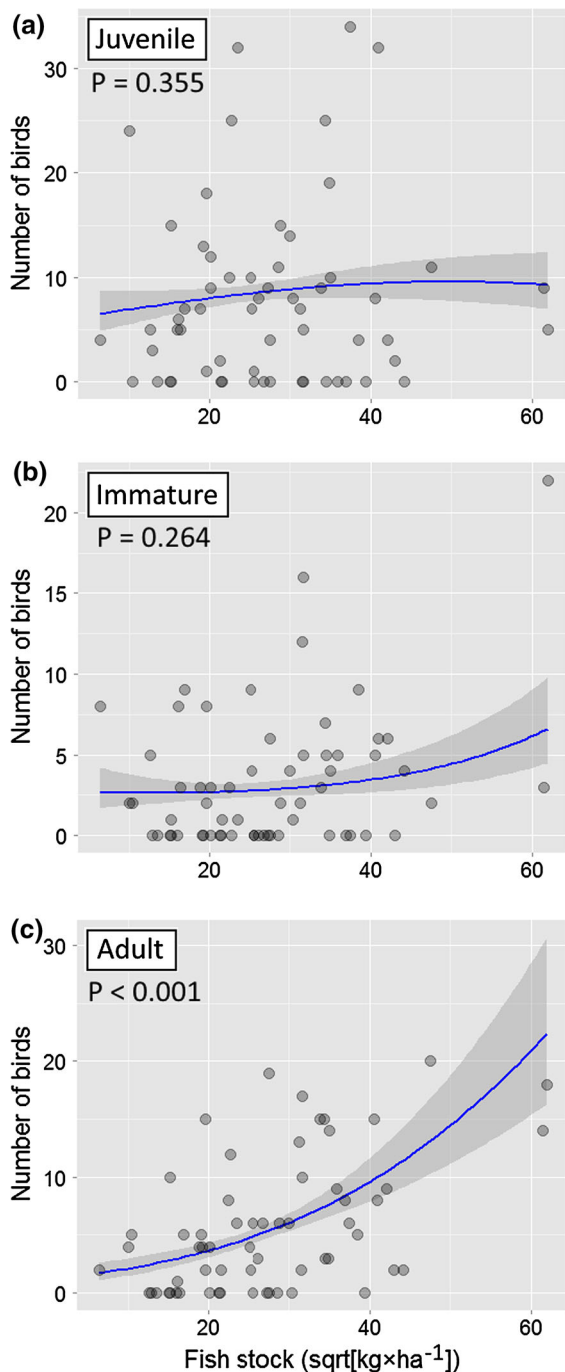


Fig. 4 Relationship between fish stock and abundance of **a** juvenile, **b** immature and **c** adult Caspian gulls. The fitted logarithmic curve with standard errors (*shaded dark strip*) are shown

variable patterns of abundance of this age class across foraging habitat patches. It is also noticeable in weights of the best models for abundance of immatures that are

lower than for models for juveniles and adults. Among environmental factors affecting abundance of immature birds forest cover had negative impact. In other studies of this species forests acted as a movement barrier across foraging patches that probably increase the cost of searching for food sources (Skorka et al. 2009). Markedly different responses of immature birds' abundance was found for river density and water cover, compared to juveniles. Surprisingly, these factors negatively affected abundance of birds from this age class, which is in contrast to former findings for adults (Skorka et al. 2009). Immature and juvenile gulls are usually dispersive and migrate across Europe (Kilpi and Saurola 1983; Kralj et al. 2014). This suggests that at this age Caspian gulls undertake extensive movements through landscape and develop spatial memory maps. Moreover, hierarchical partitioning indicated that the most important variable that correlated positively with the abundance of immature birds was the abundance of adults. It is possible that immature birds are better able than juvenile birds to successfully compete with adults and avoid kleptoparasitism and thus take advantage of social public information provided by foraging adults.

Abundance of adult birds was affected by factors acting at spatial scales similar or greater to that in immature birds. However, the effect of variables affecting abundance of adults differed from immatures and was similar to juveniles. Abundance of adults was positively correlated with water cover and river density. The explanation of this result is the same as for juveniles, however these effects acted at larger spatial scales. The variable that has the strongest impact on adult abundance was fish density (Fig. 4). This is an important finding. When prey is hardly visible in foraging patch and its density vary among patches then building spatial memory plays crucial role is foraging efficiency (Parsons and Dumont 2003; Freidin and Kacelnik 2011). Fish ponds vary in fish production but are relatively constant across years (Dobrowolski 1995). Moreover, hunting fish requires skills and substantial effort (Burger 1988; Skorka and Wojcik 2008). Thus fish density is an indicator of patch quality (Johnson 2007) and the knowledge as to which fish farms have high prey densities may give competitive advantage to individuals. Acquiring this knowledge demands time and it can be completed throughout life-span, therefore adult birds can possibly use this spatial information more effectively.

Caspian gulls hunt variety of fish, but published data suggests that the preferred species is the common carp (Gwiazda 2004; Skorka et al. 2005; Gwiazda et al. 2011). This fish is about 20 % heavier than other fish species of similar size (Gwiazda et al. 2011). Carp is the dominant fish species and other fish species are accidental in fish farms (Dobrowolski 1995). Despite the preferences to carp there is good evidence that Caspian gull can adjust their diet to local fish community and, generally, to food availability (Skorka and Wojcik 2008; Gwiazda et al. 2015). Earlier study has shown this species can also adjust prey size choice depending on foraging patch isolation metrics (Skorka et al. 2009). Nevertheless, Caspian gulls hunt fishes of different sizes ranging from 5 to 47 cm with no differences between age classes (Skorka and Wojcik 2008; Gwiazda et al. 2011). This may explain the lack of statistically significant relationship between estimates of fish size and abundances of Caspian gulls.

Despite the differential response of juvenile, immature and adult birds to the same factors and spatial scales, there were statistically significant correlations between abundances of age classes indicating that social interactions (e.g. flocking behaviour, parenting interactions occurring between juvenile and adult birds) may also be an important mechanism alongside building spatial memory maps of landscapes by individuals. Uncertainty reduction is a central adaptive problem for many species. Some group-living species have evolved effective social mechanisms for reducing uncertainties in their environments. A prime example is a system of reciprocal exchange (e.g., Axelrod 1984) and social learning (Griffin 2004). Previous studies suggest that acquisition of food preferences is heavily influenced by cultural transmission (Galef and Giraldeau 2001). Why then was not the abundance of juvenile birds perfectly correlated with adult birds? Our unpublished data indicate that Caspian gulls foraging socially express “producer–scrounger” group structure in a habitat patch (Krebs and Inman 1992; Giraldeau and Caraco 2000). Juvenile gulls gain from social learning: juveniles foraging with adults had higher gross foraging success than juveniles foraging alone, however this higher success was then quickly reduced by adults kleptoparasitism on these young birds (Skórka et al. unpublished). In result juvenile birds foraging socially had equal net foraging success as juvenile gulls foraging solitary. Kleptoparasitism is foraging tactic

characteristic for gulls performed by dominating adults towards subordinate juveniles (Carroll and Cramer 1985; Skorka and Wojcik 2008). Therefore, social groups may impose constraints on subordinate individuals by adult competition, aggression and kleptoparasitism. The aftermath may be that juvenile birds may undertake decisions to forage and seek foraging patches independently of adults and this may lead to observed pattern of response of juvenile birds to the same environmental factors but different spatial scales as compared with adult birds.

Other factors that potentially could have affected abundance of gulls in fish ponds were predatory pressure and competitive interactions with other species. We did not include potential predation pressure in this study because Caspian gull is a large bird and in the study area there was no avian predator able to hunt this gull. Also, other behavioural interactions with other species might have affected behaviour and abundance of Caspian gulls. However, counting all other waterbirds at the time of gull surveys was unfeasible in this study. It would require much more time spent on counting, more people engaged and financial resources. However, we believe that interactions with other species, e.g. competition did not affect our major findings (especially the effect of spatial scale). Competitive abilities strongly correlate with body size (Alatalo and Moreno 1987) and Caspian gull with its large body size usually ignores other species (Skorka et al. 2012).

Measurements at different radii were positively correlated between scales, but the value of the correlation decreased with distance between scales. For example water cover measured within 2.5 km radii was strongly correlated with water cover at 5 km, but much less with water cover measured within a radius of 15 km. This indicates that some landscape characteristic are predictable in space. The most predictable land cover was human settlement cover as measurements within 2.5 and 15 km were strongly correlated. However, in other landscape characteristics the correlation across scales was much lower, as in case of river density, which when measured at 2.5 km scale was uncorrelated with that measured at scale of 15 km. It also explains why settlement cover was weak predictor of bird abundance. The high predictability of human cover across spatial scales in this landscape preclude using this land cover as a good proxy of distribution of variable food resources.

Consequences for selection of scales in other studies

Different response of age classes to spatial scales has also important methodological implications. When studying habitat selection of a species with different age classes the scale should be selected separately for different age classes. For example, river density best described abundance of juvenile birds at scale of 2.5 km, but not for adults, despite this correlation being significant at the scale of 10 km.

Not only abundance of different age classes may respond to spatial scale. Males and females may also respond to the same factors, but at different spatial scales (Alves et al. 2013). There are some sexual differences in foraging tactics in gulls (Yoon et al. 2013; García-Tarrasón et al. 2015), which may result in differential response to spatial scales. However, in our study we did not control sex of birds as sex is indistinguishable in field conditions (Malling Olsen and Larsson 2004). The identification would require large-scale ringing of young birds in breeding colonies and molecular identification of their sex. Potential sex-specific response to different spatial scales interacting with age should be addressed in further studies as this may be helpful in understanding sex-specific habitat choice and survival in birds.

Conclusions

We have demonstrated that during maturation birds may respond to information about structural components of the environments gradually from fine- to large spatial scales. This suggests that building a spatial memory map follows this spatial pattern. Moreover, we have shown that knowledge about location of high quality habitat patches requires time thus probably only older birds can respond to such spatial variation in resources. Interestingly, strong association between ages and possible social learning does not generate such response in younger age classes. Juvenile and immature gulls undertake long-distance natal dispersal. It is intriguing how these long-distance migration relate to fine-scale numerical response of juvenile birds to landscape characteristics. It is possible that seeking foraging patches is a process independent from directional autumn dispersal and migration. This study also underlines the role of certain types of land

covers (waters, rivers) as movement corridors for even such mobile animals as studied species.

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