Residency and a broad feeding spectrum are related to extensive spatial exploration in parrots

Claudia Mettke-Hofmann[1,2,*], Michael Wink[3], Michael Braun[3] & Hans Winkler[4]

[1]School of Natural Sciences & Psychology, Liverpool John Moores University, United Kingdom; [2]Max-Planck Institute for Ornithology, Department of Migration and Immuno-Ecology, Radolfzell, Germany; [3]Institute of Pharmacy and Molecular Biotechnology, Heidelberg University, Germany; [4]Konrad-Lorenz-Institute for Comparative Ethology, Vienna, Austria

* Corresponding author: School of Natural Sciences & Psychology, Liverpool John Moores University, James Parsons building, Byrom Street, Liverpool L3 3AF, United Kingdom

Email: C.C.Mettke-Hofmann@ljmu.ac.uk; phone: +44-151-231-2247

Data were collected while CM-H was a postdoc at Free University of Berlin, Department of Behavioural Biology in collaboration with the Max-Planck Institute for Ornithology, Department Vogelwarte Radolfzell and Konrad-Lorenz Institute for Comparative Ethology, Vienna. Analyses were conducted at Liverpool John Moores University, School of Natural Sciences & Psychology.

Abstract

Resident and nomadic species differ substantially in their mobility with the former spending most of their life in a restricted area and the latter encountering many areas while tracking spatiotemporal unpredictable resources. Earlier studies have shown that information gathering differs alongside this mobility axis – resident species pay more attention to changes in their familiar environment than nomadic ones. However, little is known about spatial exploration in resident and nomadic species. We investigated spatial exploration in 10 closely related parrot species that differed in their mobility by giving them access to two unfamiliar aviaries left and right of the familiar aviary. For analyses, mobility and some diet and habitat variables were related to spatial exploration. Nomadic species spent less time exploring the novel aviaries and also started tactile exploration later than resident/nomadic and pure resident species. Furthermore, diet specialists visited more new locations in relation to their overall movements than diet generalists. The variables were not correlated with the molecular phylogeny (mitochondrial cytochrome b) of the species. The results indicate that nomads invest less in spatial exploration than residents possibly because they stay only for limited periods of time in one particular area or use easier to assess cues. Residents, in contrast, assess a novel environment in detail as they may collect information about future breeding sites for which they need short- and long-term information. Finally, diet specialists may pay attention to fewer environmental cues than generalists which allows them to move faster through a novel environment.

Keywords: Psittacidae, neophilia, nomads, birds, phylogeny

Introduction

Birds are among the most mobile vertebrates due to their ability to fly. However, there are large differences in space use between bird species with one of the most striking differences found between resident species, on the one hand, and more mobile species such as migrants or nomads, on the other hand. These differences in space use have evolved in adaptation to differences in resource availability and predictability. Residency is favored in predictable environments and species following this lifestyle are often found in vegetation types that are stable throughout the year (e.g. coniferous vegetation; Mac Arthur 1959; Airola and Barrett 1985; Sage and Robertson 1996). They also rely on predictable food sources (Brown and Hopkins 1996) in a relatively restricted area. These may either be permanently available food resources or reoccurring resources in a subannual or annual cycle (Brown and Hopkins 1996).

Migration and nomadism evolved in adaptation to spatiotemporal variation in resources on a much larger scale (Jonzen et al. 2011) by taking advantage of resources in widely separated areas. Here, migration evolved in response to highly predictable and seasonal resources that allowed evolution of ‘hardwired’ and endogenously controlled migrations between widely separated but predictable breeding and nonbreeding sites (Gwinner 1996). Nomadism, in contrast, is favored by highly variable and unpredictable resources in space and time resulting in large intervals between successive good years in an area and cyclic rather than random fluctuations (Andersson 1980). Nomadic species take advantage of temporary superabundant food resources that are unpredictable in time and space (Brown and Hopkins 1996; Dean 1997; McGoldrick and Mac Nally 1998). As a consequence, their habitat selection is only short-term for the duration of favorable environmental conditions. Often that may not exceed the duration of one breeding cycle. For the short-term, these habitats are relatively stable, in the long-term however, they are extremely variable and unpredictable. Nomads use environmental cues to track resources over large areas and show very flexible movement patterns (Allen and Saunders 2002; Reside et al. 2010) though it is currently not known which cues they use and in which detail they assess their environment (Jonzen et al. 2011).

Differences in mobility have been shown to be related to cognitive abilities such as higher innovation rates in resident species as compared to migratory ones (Sol et al. 2005). In contrast, migrants have better spatial memory abilities (Cristol et al. 2003; Mettke-Hofmann & Gwinner 2003; Pravosudov et al. 2006) and often associated with these larger hippocampi or more neurons in this brain area than residents (Healy et al. 1996; Cristol et al. 2003; Pravosudov et al. 2006). Moreover, differences in information gathering have been found. For example, during the non-breeding season (winter) resident Sardinian warblers (*Sylvia melanocephala*) explored changes in their familiar environment more than closely related but migratory garden warblers (*S. borin*; Mettke-Hofmann 2007). Similar differences were found in ten closely related resident and nomadic parrot species during courtship stage (Mettke-Hofmann et al. 2005). The differences in information gathering were explained with different cost/benefit considerations for residents and more mobile species. In brief, residents benefit by investigating changes in their familiar environment as they may indicate the emergence of new resources. As residents are restricted to a relatively small home range tracking resources throughout the year is of paramount importance. Nomads and migrants, in contrast, benefit little from investigating changes in their familiar environment as they spend only limited periods of time at a given location (ranging from days during stopover to months during wintering (migrants) or breeding (nomads); for a more detailed discussion see Mettke-Hofmann et al. 2005; Mettke-Hofmann 2007).

The same two warbler species mentioned above also differed in the exploration of an unfamiliar environment (spatial exploration) in fall; the resident Sardinian warbler explored a novel environment in more detail than the migratory garden warbler (Mettke-Hofmann & Gwinner 2004; Mettke-Hofmann et al. 2009) which is initially surprising given that migrants regularly encounter unfamiliar environments whereas residents rarely leave their familiar site. However, during the post-breeding period residents may explore an unfamiliar site in search of a new territory and need detailed information about its short- and long-term suitability (Cadiou 1999; Reed et al. 1999), whereas migrants stay for only short periods at each stopover site and a rough overview about resources and threats seems to be sufficient (Moore et al. 1990; Aborn and Moore 1997; Mettke-Hofmann and Gwinner 2004). Currently, there are no studies available comparing spatial exploration in resident and more wide-ranging species (migrants or nomads) at the beginning of the breeding season when all species are in a similar motivation to find a breeding site. The current study investigates spatial exploration in resident and nomadic parrot species at the beginning of the breeding season.

Whereas it is expected that residents need to explore a new environment thoroughly as detailed above, there are two scenarios of spatial exploration in nomads. On the one hand, as nomads stay only for limited periods of time at each site, gathered information can only be used in the short-term for the time staying at this particular site. Furthermore, exploring a site for the presence of superabundant food may not require long-lasting and detailed exploration as such resources are very conspicuous due to their clumped occurrence. From a cost/benefit approach, one may, therefore, expect that spatial exploration in nomads evolved to be relatively short-lasting and possibly superficial. On the other hand, even though nomads leave a site when conditions deteriorate they may remain at a particular site for one or several breeding attempts (McGoldrick and Mac Nally 1998) and a more detailed assessment of the environment may be beneficial. This may be a one-off detailed assessment of an unfamiliar environment to allow settlement decisions (for or against breeding) as once familiarized with a site nomads have been shown to explore changes in the familiar environment only superficially (Mettke-Hofmann et al. 2005) as nomads leave sites when conditions change (see above). It is therefore, also possible that nomads evolved detailed spatial exploration to assess a new site.

In the current study, spatial exploration was compared between ten closely related resident and nomadic parrot species from the Autralasian region. Based on the above considerations two hypotheses were formulated. Firstly, following scenario one it was hypothesized that nomads explore a novel environment for a shorter period of time and in less detail than closely related residents (as outlined above residents were expected to explore a novel environment at length and thoroughly; Mettke-Hofmann and Gwinner 2004). Secondly, following scenario two it was hypothesized that nomads explore a novel environment at similar length and in similar detail as residents.

The ten parrot species under investigation belonged to two tribes, one representing a nectarivorous/ frugivorous group and the other a primarily seed-eating group. Within each tribe species differed in their mobility (resident – nomadic). Testing representatives from two tribes allowed assessing the relationship between mobility and spatial exploration as a factor independent of feeding specializations. Exploratory behavior is heritable as has been shown in selection line and genetic studies of birds and mammals (Drent et al. 2003; Powell et al. 2003). Therefore, possible differences in exploration are thought to have evolved as an adaptation to a species' ecology and mobility. Learning about spatial information gathering in residents and nomads helps to get a better understanding how life-history traits such as nomadism and residency are related to information gathering.

Material and Methods

Experimental birds and housing

Experimental birds included 79 adult pairs (74 entered the analysis; see below) belonging to ten parrot species (see Table 1 for sample sizes). Most pairs consisted of a male and a female; only seven were of the same sex (including five pairs of the Emerald Lorikeet, *Neopsittacus pullicauda*, the sexes of which were not known before the experiment). All birds were borrowed from private breeders who were well known to us (C. M.-H.) or highly recommended by other breeders. Only birds kept in sufficiently large aviaries were chosen. Pairs (same and different sexes) had already been established for at least several months. Six species belonged to the Loriini and four species to the Platycercini. All Platycercini and most of the Loriini were descendents of several generations of captive-bred birds. Imported birds that had lived for several years in captivity were included among the Emerald lorikeet and the three *Charmosyna* species.

Both tribes have their origin in the Australasian region. Representatives of the Loriini primarily feed on nectar, pollen and fruits but to some extent also incorporate seeds, vegetable matter and insects into their diet. They inhabit open habitats with trees, forests and forest edges (Meyer and Wiglesworth 1897; Bell 1966; Coates 1985; Forshaw 1977; Forshaw 1988; observations by C. M.-H.). Platycercini are mainly seed-eaters of grass and herbaceous plants and feed to a lesser extent on insects, pollen, nectar and vegetable matter. They prefer open habitats with trees and forest edges (Lea and Gray 1935; Boehm 1959; Fleming 1974; Forshaw 1977; Forshaw 1988; observations by C. M.-H.). For a detailed description of distribution, diet and habitat use see Mettke-Hofmann et al. (2005). The migratory behavior was assessed from the literature (Meyer and Wiglesworth 1897; Rand and Gilliard1967; Bell 1982; Coates 1985; Forshaw 1988). Observation in the field (C. M.-H., pers. obs., Schodde, pers. comm.) indicated that Rainbow Lorikeets (*Trichoglossus haematodus moluccanus*) are sedentary in the northern part of their range but become more and more nomadic towards the south. Mulga parrots (*Psephotus varius*) are sedentary in the center of their distribution and nomadic at its edges. Since origin could not be ascertained both species were classified as resident as well as nomadic (Fig. 1).

Data collection was carried out between May and August in three consecutive years. Pairs were transferred for 18 days in 2 x 2 x 2 m outdoor aviaries with three perches, a breeding box and sand on the ground. Three sides of each aviary were covered with reed mats on the outside. Food and water were available *ad libitum*. The Loriini were fed a well established diet of pollen, fruit sugar and honey (for details see Mettke-Hofmann et al. 2005). The Platycercini were kept with a mixture of seeds (for details see Mettke-Hofmann et al. 2005). Additionally, we offered half-ripe millet in ears. All birds had ten days to habituate to the aviary. At the end of this period, all pairs were in courtship state except those consisting of the same sex. For half of the pairs, equally distributed among the species, the spatial exploration test was conducted on day 11. The other half received this test on day 18 after being tested on an object exploration test on days 11 and 14 (Mettke-Hofmann et al. 2005).

Experimental procedure

For the experiment, one hour after food had been given at dawn two 1 x 1m large panels left and right of the main aviary were simultaneously removed to give access to two samesized aviaries (2 x 2 x 2 m) which differed in the arrangement of perches and the nest box from the main aviary. No food was available in the novel aviaries. Observation started with removal of the panels and lasted for six hours. Only the first bird entering one of the two unfamiliar aviaries was followed and all movements and behaviors in the novel aviary were continuously recorded on a tape recorder. To assess movement through the novel aviary, 45 locations were distinguished in each aviary. Birds could land on all walls (front, rear, left, right), the ceiling, bottom and five perches. Six rectangles each were distinguished for the front and rear wall (left – middle – right, upper and lower part), ceiling and bottom (left – middle – right; front and rear part) and four each for the left and right wall (upper – lower; front – rear). Three perches traversing the entire aviary were divided into left – middle – right and one short perch each was located in the rear corners of the aviary. Finally, birds could land on the nest box or perch in front of the nest box.

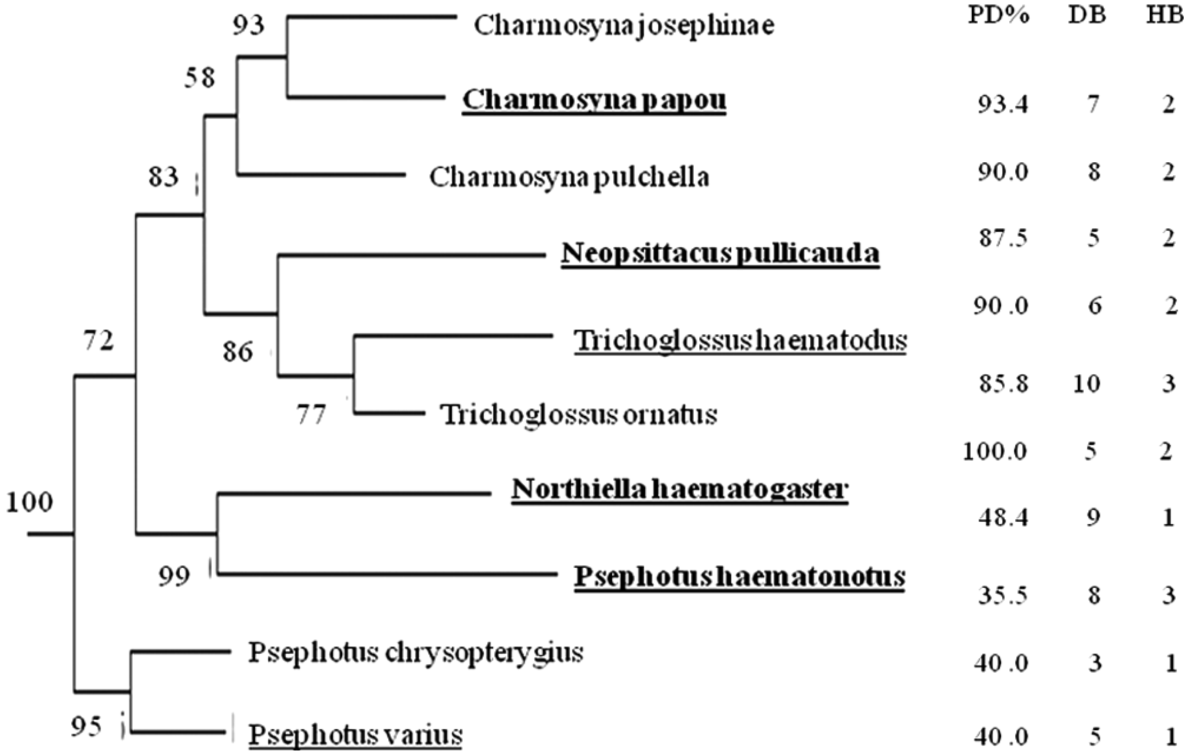

Fig. 1: Molecular phylogeny of parrots with distribution of mobility and ecological variables
Using nucleotide sequences of cyt b a phylogeny was reconstructed by Maximum-Likelihood (Nearest-Neighbor-Interchange). Numbers at branches refer to bootstrap values from 600 replications.
Bold and underlined: resident, underlined: resident/nomadic, rest: nomadic; PD%: percentage of patchily distributed food in the diet; DB: diet breadth; HB: habitat breadth

Analyses

We had to exclude five pairs from analyses because one turned out to be juvenile (juveniles are generally more explorative than adults, Vince 1960; Greenberg and Mettke-Hofmann 2001) and the others not be healthy (Table 1).

Table 1: Test species

Tribe	Species	Sample size
Loriini	*Trichoglossus ornatus* (Ornate Lory)	7 (6)*
	Trichoglossus haematodus moluccanus (Rainbow Lory)	7 (7)
	Neopsittacus pullicauda (Emerald Lorikeet)	7 (7)
	Charmosyna josephinae (Josephine´s Lory)	7 (7)
	Charmosyna papou goliathina (Papuan Lory)	8 (8)
	Charmosyna p. pulchella (Fairy Lorikeet)	6 (6)
Platycercini	*Psephotus chrysopterygius dissimilis* (Hooded Parrot)	9 (8)
	Psephotus varius (Mulga Parrot)	7 (7)
	Psephotus haematonotus (Red-rumped Parrot)	12 (11)
	Northiella haematogaster (Blue Bonnet)	9 (7)

*Numbers in brackets represent sample size (in pairs) in analysis

Three measures of spatial exploration were taken; 1) Time spent exploring the novel aviaries (the sum of time looking around, moving in the novel aviary and exploring walls, the nest box, perches etc. with the beak) as an overall measure of spatial exploration. For this variable data from both aviaries were combined as there was no interaction between duration of exploration of the first and second aviary and mobility (repeated ANOVA was used with duration of exploration in the first and second aviary as repeated measure (within factor) and mobility as independent factor; within factor $F_{1,8}$ =7.724, P=0.027 (the second aviary was generally explored for a shorter time than the first one); mobility $F_{2,7}$=6.153, P=0.029 (nomads explored overall less than residents and residents/migrants); interaction within factor x mobility $F_{2,7}$=0.120, P=0.888 (exploration of the first and second aviary did not differ between residents and nomads). Any differences in spatial exploration in relation to mobility found in the main analysis (see below) are therefore, not caused by differences in exploration of the first and second aviary. Furthermore, 2) latency to start tactile exploration (time to start manipulating reed mats, perches or the nest box with the bill after the new aviary had been entered) was taken as a measure of a more detailed tactile exploration of the aviary (Todt et al. 1992). 3) The proportion of new locations visited in relation to all movements of a bird was calculated to measure how quickly the new aviary was assessed (Verbeek et al. 1994; Mettke-Hofmann et al. 2009). The proportion of areas visited was only assessed for the first 30 minutes spent in the first new aviary as sample size started to decrease afterwards (all birds explored for 30 minutes but not all continued for much longer). The overall number of movements and the number of new areas visited was assessed for each of the first five minutes, and the 10th, 15th, 20th, 25th and 30th minute. The proportion of new areas visited was calculated for each minute and then the mean taken across all minutes.

Each of the three dependent variables was tested against five (four for proportion of new locations visited) independent variables with a regression analysis. Variables were selected with a stepwise procedure with variables entered or removed depending on the strength of their correlation with the dependent variable. The first variable entered shows the highest correlation. After each step each variable is checked again. Only those variables remain in the model that significantly add to the explained variance (Brace et al. 2006). Independent variables were mobility and three ecological variables which may also influence spatial exploration as well as a measure for activity. We divided mobility into three categories: nomadic, nomadic/resident (species includes resident as well as nomadic populations), resident. Furthermore, two variables describing diet were included - patchiness and diet breadth (Fig. 1). Diet breadth represented the number of different food types included in a species' diet out of 10 (for details about food types see Mettke-Hofmann et al. 2005). For patchiness the percentage of patchily distributed food types (nectar, pollen, blossoms, fruits, tree seeds, buds) in a species' diet was calculated from the percentage of such food types in the diet of a species (Mettke-Hofmann et al. 2005). Both, diet specialization and patchily distributed food may favor more spatial exploration (Allen and Saunders 2002). Furthermore, habitat breadth was included representing the number of habitats out of four used by a species (for details about habitats see Mettke-Hofmann et al. 2005). Finally, activity of an individual may have an effect on duration of exploration of an unfamiliar environment or latency to explore tactile. Activity levels of the first bird were assessed during one hour in the morning on a day without experiments. Positions of the bird were recorded every minute and moves per minute calculated. Species' means were used for the analysis. The third dependent variable (proportion of new locations visited in relation to all movements) was already corrected for movements and therefore, activity was not included in this analysis. Independent variables were not correlated with each other (all $r<0.5$, $P>0.15$) except for mobility and diet breadth which were marginally correlated ($r=0.63$, $p=0.050$) with nomadic species having a more specialized diet. Time spent exploring and latency to start tactile exploration were log10 transformed to get normally distributed data.

Phylogenetic relationships

Phylogenetic relationships may have an influence on reactions (Harvey and Pagel 1992). However, earlier studies on the same species have shown that residency and nomadism evolved independent from phylogenetic relationships as an adaptation to the particular conditions a species has been exposed to (Mettke-Hofmann et al. 2005). For the current study, a better supported tree was used (though phylogenetic relationships remained the same as during the former study). DNA was isolated from muscle or scale tissue, which was preserved in ethanol, using a standard phenol/chloroform protocol (Sambrook and Russel 2001).

PCR amplifications of the mitochondrial cytochrome b gene were performed with 50 µl reaction volumes containing 1 × PCR buffer (Bioron, Ludwigshafen, Germany), 100 µM dNTPs, 0.2 units of Taq DNA polymerase (Bioron, Ludwigshafen, Germany), 200 ng of DNA, and 5 pmol of primers. Thermal cycling was performed under the following conditions: (1) an initial denaturing step at 94 °C for 5 min; (2) 35 cycles: 1 min at 94 °C, 1 min at 52 °C, and 1 min at 72 °C; and (3) a final 5-min extension at 72 °C. PCR products were precipitated with 4 M NH_4Ac and ethanol (1:1:6) and centrifuged for 15 min (13,000 rpm). Sequencing was carried out on an ABI 3730 automated capillary sequencer (Applied Biosystems) with the ABI Prism Big Dye Terminator Cycle Sequencing Ready Reaction Kit 3.1 by STARSEQ GmbH (Mainz, Germany).

Phylogenetic analyses

Phylogenetic analyses were performed with MEGA 5.0 (Tamura et al. 2011) using Maximum likelihood method with the substitution model Tamura-Nei. For tree interference Nearest-Neighbor-Interchange (NNI) was applied. Bootstrap calculations were carried out with 600 replications.

The tree was used to visualize the relationship between phylogeny and the four ecological factors (Fig. 1). None of the independent factors explaining spatial exploration (mobility, diet breadth; see below) showed a relationship to phylogeny. In an earlier study including the same species, mobility has been shown to be independent of phylogenetic relationships

(Mettke-Hofmann et al. 2005). Similarly, here even within closely related sister taxa, one species can be a diet specialist and another one a diet generalist (Fig. 1). Therefore, with respect to the factors investigated here species were considered as independent data points.

Housing conditions and experiments were in accordance with German institutional guidelines and legal requirements. All birds had valid CITES certifications.

Table 2: Results from the regression analyses for duration of spatial exploration, latency to start tactile exploration and the proportion of new locations visited

	Duration of spatial exploration		Latency tactile exploration		Proportion new locations visited	
Independent var.	t-value	p-value	t-value	p-value	t-value	p-value
Mobility	2.414	**0.042**	-2.427	**0.041**	-0.987	0.356
Diet breadth	0.173	0.868	-0.537	0.608	-3.270	**0.011**
Patchiness of food	-1.190	0.273	2.322	0.053	-0.474	0.650
Habitat breadth	-0.125	0.904	0.087	0.933	0.156	0.880
Activity	0.595	0.570	-0.654	0.534		

Bold values indicate variables selected in the model

Results

Duration of spatial exploration in the novel aviaries showed a relationship to mobility which explained 35% of the variance (r^2=0.349, $F_{1,8}$=5.826, P=0.042). Nomadic species explored the aviaries on average for a shorter time than resident/nomads and residents (Fig. 2). No other variable had a significant effect (Table 2). Furthermore, latency to start tactile exploration showed a significant relationship to mobility which explained 35% of the variance (r^2=0.352, $F_{1,8}$=5.892, P=0.041). Nomads started tactile exploration later than resident/nomads and residents (Fig. 3). No other variable was entered (Table 2). Finally, the mean proportion of new areas visited in relation to all movements was related to diet breadth which explained 52% of the variance (r^2=0.519, $F_{1,8}$=10.693, P=0.011). Species with a small diet breadth visited relatively more new areas than species with a broader diet (Fig. 4). No other variable had an effect (Table 2).

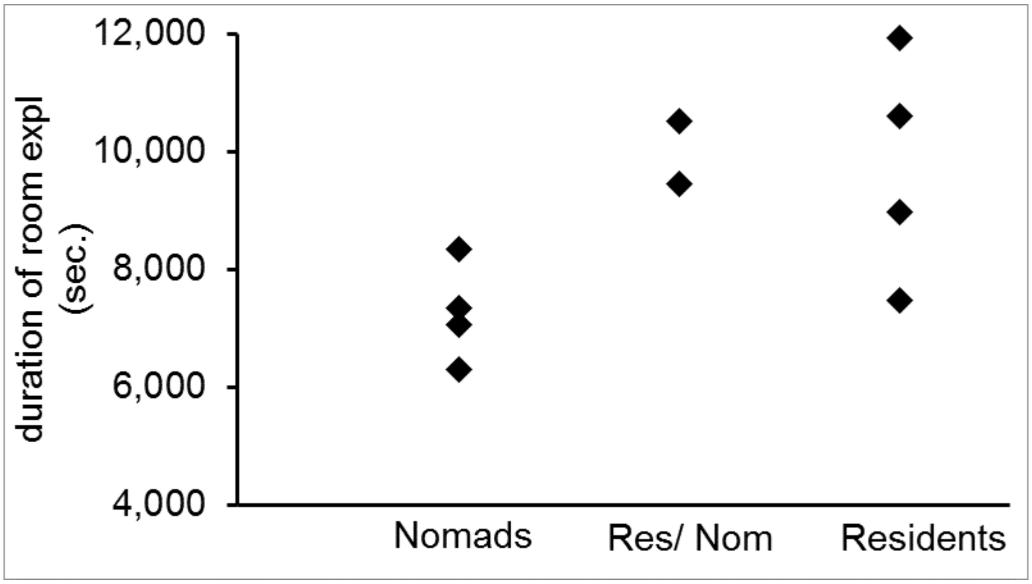

Fig. 2: Time spent exploring the two novel aviaries in relation to mobility
Time spent exploring (sec) is plotted against mobility
Res/nom: resident/nomadic; expl.: exploration

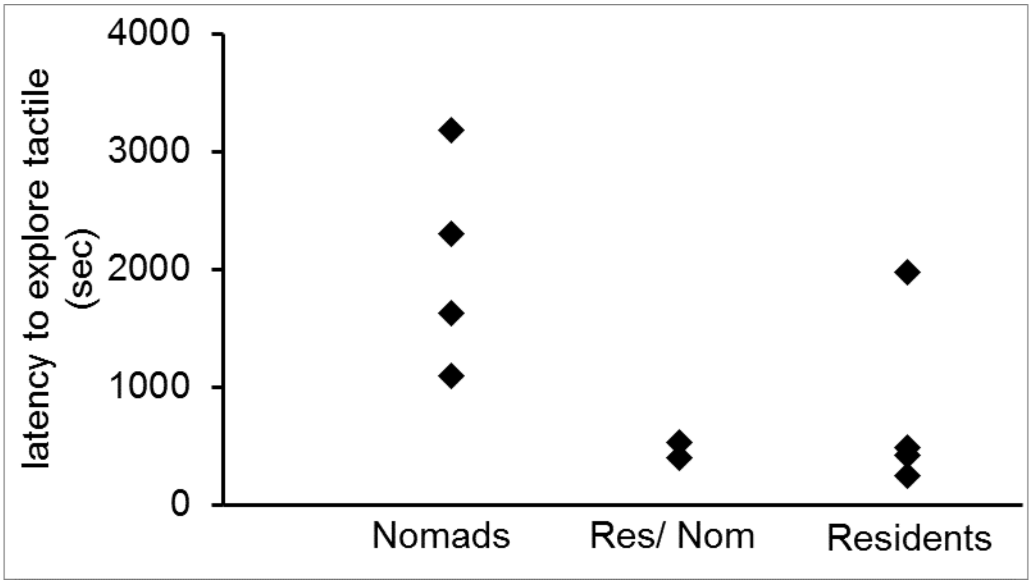

Fig. 3: Latency to start tactile exploration in the novel aviaries in relation to mobility
Latency to start tactile exploration (sec) is plotted against mobility
Res/nom: resident/nomadic

Discussion

The study investigated spatial exploration during courtship stage in several parrot species in relation to a species' mobility and some ecological factors. Nomadic species explored two novel aviaries for a shorter period of time and started tactile exploration later than resident/nomadic or resident species. Diet specialists visited relatively more new areas in the aviaries than diet generalists.

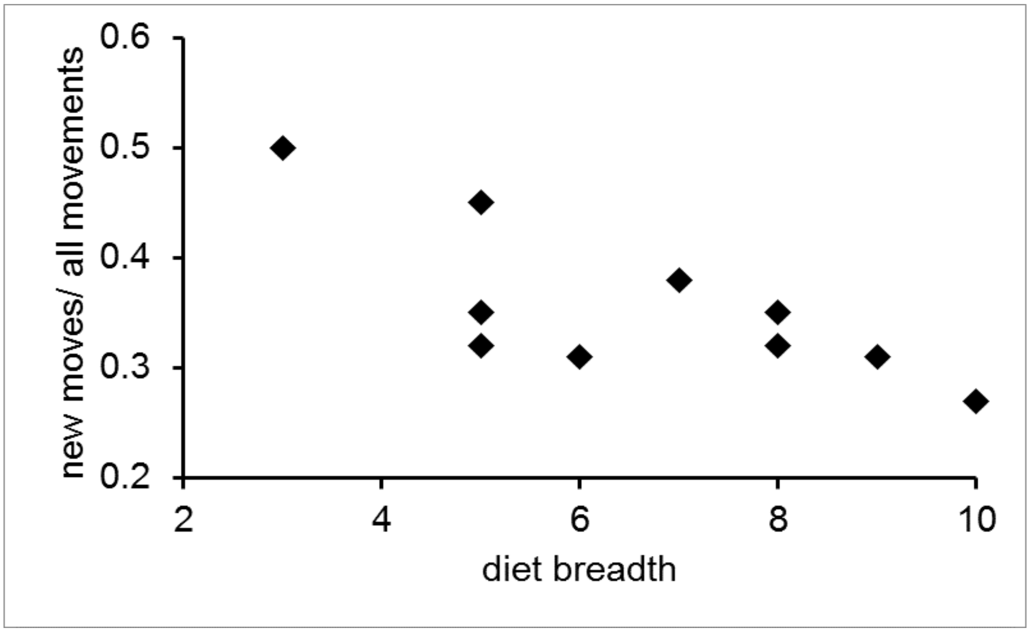

Fig. 4: Proportion of new areas visited in relation to diet breadth
Proportion of new areas visited relative to all movements is plotted against diet breadth
Numbers on the x-axis indicate the number of different food types out of 10 used by a species

The first two findings support the first hypothesis. Nomadic species invested less in spatial exploration both, in terms of the overall duration of exploration and the onset of tactile exploration which is a measure of a more detailed assessment of the environment (Todt et al. 1992) as compared to resident/ nomadic and resident species. Nomadic species stay for only limited periods of time at each site and a longer lasting and more detailed exploration may bear more costs than benefits as information cannot be used in the long-term (Mettke-Hofmann et al. 2005). Furthermore, nomads may not need long to check on cues relevant for decisions whether to settle or not. For example, superabundant food is likely to be very conspicuous and usually clumped and its presence or absence quickly discovered. To be fully informed about relevant cues may therefore, take shorter in nomads than in residents.

The finding that nomads spent less time in spatial exploration than residents is in line with results in several other species which differ in their movement patterns. Migratory garden warblers explored a novel environment less than resident Sardinian warblers when tested in fall (Mettke-Hofmann & Gwinner 2004; Mettke-Hofmann et al. 2009). Furthermore, spatial exploration in young birds and mammals correlates with dispersal patterns. Wild caught young great tits (*Parus major*) that later settled near their place of birth explored an unfamiliar environment in the laboratory longer and in more detail than tits that dispersed further (Dingemanse et al. 2003). In flying squirrels (*Pteromys volans*), long-distance dispersers which could not reach their future breeding site during exploration trips had fewer exploration trips prior to dispersal than short-distance dispersers and philopatric individuals which settled within the range of their exploration trips. It was concluded that the short-distance dispersers and philopatric individuals could use the information for future settlement decisions, whereas long-distance dispersers might have gained little from exploring the natal area as they later moved away (Selonen and Hanski 2006). It therefore, seems that time-restricted use (ranging from days to months) of an area favors short-lasting exploration.

However, regarding the current study a cautionary note should be added. The current experimental design may have simulated exploratory flights from a still suitable site to nearby new sites to learn about future sites rather than simulating an actual move to a new site. Once the individual decides to vacate a given site and moves on it may assess a new site in more detail after arrival. Alternatively, nomads may use heterospecific information about breeding opportunities as has been shown in several migratory species (Mönkkönen et al. 1997). More research into the final assessment of a site in nomads once individuals have moved is needed to clarify this point.

For the resident species the experimental setup likely simulated access to a neighboring territory. If so, residents not only need short-term but also long-term information about a possible future territory (Cadiou 1999; Reed et al. 1999; Mettke-Hofmann and Gwinner 2004) as they stay year-round in a particular area. Alternatively, even if they have seen the new aviaries just as an enlargement of their current territory a more detailed assessment about nesting opportunities, food availability and hiding places (birds of prey were regularly seen flying close to the aviaries causing flight behavior) seems to be beneficial.

The two species which could be resident or nomadic behaved more like residents. This is surprising as the same individuals showed intermediate exploration patterns when confronted with novel objects in their familiar environment (Mettke-Hofmann et al. 2005). This indicates that species that are partially nomadic invest more in spatial exploration than pure nomads possibly to find out whether the site is suitable for permanent settlement. The increased costs of a more detailed spatial exploration could be out-weighted by benefits of long-term settlement. However, more research is needed into this issue.

Movement through the new aviaries was related to diet breadth with more specialized foragers visiting relatively more new areas in the aviary than less specialized ones. This indicates that diet specialists assess a novel environment faster (Verbeek et al. 1994) and as a consequence possibly more superficially than diet generalists as there is usually a speed-accuracy trade-off (Chittka et al. 2003; Rival et al. 2003). Tebbich et al. (2009) investigated object exploration in Darwin finches. Diet generalists were more likely to approach a novel object in their familiar environment than diet specialists. This corroborates with a possibly more accurate assessment of a novel environment in the generalists in the current study. Diet specialists may be able to move faster through an unfamiliar environment as they only have to pay attention to a few cues that indicate the presence of their specialized food, whereas diet generalists have to consider a broader range of cues and their relative abundance (Bernays 1998). A narrowed down field of attention to a few relevant cues has been shown in more specialized Apple sawflies (*Hoplocampa testudinea*) and apple maggots (*Rhagoletis pomonella*) as compared to more generalist Tarnished plant bugs (*Lygus lineolaris*; Prokopy and Owens 1978). Furthermore, there is a broad range of literature showing that at least in insects diet specialists are faster in decision-making than diet generalists as the former have to pay attention to fewer cues than the latter (e.g. Bernays 1998; Troncoso et al. 2005). Unfortunately, there is no comparable vertebrate literature available to this topic. Interestingly, in the current study diet breadth and mobility were correlated with diet specialists often being nomadic. This supports the idea mentioned above that even though nomads invest less time in spatial exploration their environmental assessment with respect to relevant cues for decision-making may be as thorough as in residents as they have to pay attention to fewer or more conspicuous cues than residents.

All birds tested in this study on spatial exploration have also been tested on their reaction to a novel object in their familiar environment (object exploration; Mettke-Hofmann et al. 2005). There is increasing evidence that spatial and object related information is learned and processed differently. For example, the hippocampal formation is an important brain region for processing spatial information. Damage to this region does impair spatial learning but not object-related learning (e.g. Sherry and Vaccarino 1989; Hampton and Shettleworth 1996). Furthermore, the right eye system shows a preference for object-specific cues, whereas the left eye system for spatial cues (Clayton and Krebs 1994). Finally, species that rely to a different degree on spatial information (e.g. food-storer and non-storer) differ in the kind of information stored - spatial or object-related (Brodbeck 1994). The current study is therefore, the first one providing insight how nomads assess a novel environment and how this differs in relation to closely related but resident species. In the current study, nomadic species invested less in exploration of an unfamiliar environment than resident species and this was also the case when confronted with changes (a novel object) in the familiar environment (Mettke-Hofmann et al. 2005). Taken these findings together, it seems that nomadic species are overall less exploratory than resident species; the reasons for this are likely differences in cost/benefit considerations of information gathering with nomads having only short-term benefits, whereas residents having short-and long-term benefits (see introduction and discussion above and Mettke-Hofmann et al. 2005).

In conclusion, nomadic species invested less time in spatial exploration and also explored in less detail (tactile exploration) than closely related resident species. This finding is in line with spatial exploration patterns in other species which differ in mobility and supports the idea that time restricted use of an area may favor the evolution of short and possibly superficial spatial exploration, whereas residency may favor the evolution of longer-lasting and detailed exploration. However, as nomads also tended to be diet specialists their decision-making may not be compromised by lack of information as specialists often have to pay attention to fewer relevant cues.

Funding

This work was supported by the Deutsche Forschungsgemeinschaft (DFG) (Me 1340 / 1-1 to C. M-H.).

Acknowledgements

Many thanks are owed to the numerous private breeders who put their birds at C. M.-H.’s disposal and to G. Hofmann, who arranged most of the contacts with the breeders and helped during the experiments. We are very grateful to the late E. Gwinner for providing the testing area and financial support and Bernd Leisler for supervisory support to C.M.-H. throughout the study.

References

Aborn DA, Moore FR. 1997. Pattern of movement by summer tanagers (*Piringa rubra*) during migratory stopover: a telemetry study. Behaviour. 134:1077-1100.

Airola DA, Barrett RH. 1985. Foraging and habitat relationships of insect-gleaning birds in a Sierra Nevada mixed-conifer forest. The Condor. 87:205-216.

Allen CR, Saunders DA. 2002. Variability between scales: Predictors of nomadism in birds of an Australian Mediterranean climate ecosystem. Ecosystems. 5:348-359.

Andersson M. 1980. Nomadism and site tenacity as alternative reproductive tactics in birds. J Anim Ecol. 49:175-184.

Bell HL. 1966. Some feeding habits of the Rainbow lorikeet. Emu. 66:71-72.

Bell HL. 1982. A bird community of lowland rainforest in New Guinea. I. Composition of density of the avifauna. Emu. 82:24-41.

Bernays EA. 1998. The Value of Being a Resource Specialist: Behavioral Support for a Neural Hypothesis. Am Nat. 151:451-464.

Boehm EF. 1959. Parrots and Cockatoos of the Mount Mary plains, South Australia. Emu. 59:83-87.

Brace N, Kemp R, Snelgar R. 2006. SPSS for Psychologists, 3rd edition, Palgrave Macmillan London, UK.

Brodbeck DR. 1994. Memory for spatial and local cues: A comparison of a storing and a non-storing species. Anim Learn & Behav. 22:119-133.

Brown ED, Hopkins MJG. 1996. How New Guinea rainforest flower resources vary in time and space: implications for nectarivorous birds. Austr J Ecol. 21:363-378.

Cadiou B. 1999. Attendance of breeders and prospectors reflects the quality of colonies in the Kittiwake *Rissa tridactyla*. Ibis. 141:321-326.

Chittka L, Dyer AG, Bock F, Dornhaus A. 2003. Bees trade off foraging speed for accuracy. Nature. 424:388.

Clayton NS, Krebs JR. 1994. Memory for spatial and object-specific cues in food storing and non-storing birds. J Comp Physiol A. 174:371-379.

Coates BJ. 1985. The birds of Papua New Guinea Vol. 1 Non-passerines. Alderley: Dove Publications Pty Ltd.

Cristol DA, Reynolds EB, Leclerc JE, Donner AH, Farabaugh CS, Ziegenfus CWS. 2003. Migratory dark-eyed juncos, Junco hyemalis, have better spatial memory and denser hippocampal neurons than nonmigratory conspecifics. Anim Behav. 66:317-328.

Dean WRJ. 1997. The distribution and biology of nomadic birds in the Karoo, South Africa. J Biogeo. 24:769-779.

Dingemanse NJ, Both C, van Noordwijk AJ, Rutten AL, Drent PJ. 2003. Natal dispersal and personalities in great tits (*Parus major*). Proc R Soc Lond B. 270:741-747.

Drent PJ, van Oers K, van Noordwijk AJ. 2003. Realized heritability of personalities in the great tit. Proc R Soc Lond B. 270:45-51.

Fleming A. 1974. Feeding habits of red-rumped parrots. Austr Bird Watcher. 5:184.

Forshaw JM. 1977. Parrots of the World. Neptune: T.F.H. Publications, Inc..

Forshaw JM. 1988. Australian Parrots. 2nd ed. Sydney, Auckland, Hong Kong, Chicago: Lansdowne Editions.

Greenberg R, Mettke-Hofmann C. 2001. Ecological aspects of neophobia and neophilia in birds. Curr Orn. 16:119-178.

Gwinner E. 1996. Circadian and circannual programmes in avian migration. J Exp Biol. 199:39-48.

Hampton RR, Shettleworth SJ. 1996. Hippocampal lesions impair memory for location but not color in passerine birds. Behav Neurosci. 110:831-835.

Healy SD, Gwinner E, Krebs JR. 1996. Hippocampal volume in migratory and non migratory warblers: effects of age and experience. Behav Brain Res. 81:61-68.

Harvey PH, Pagel MD. 1992. The Comparative Method in Evolutionary Biology. Oxford University Press, Oxford, New York, Tokyo.

Jonzen N, Knudsen E, Holt RD, Saether BE. 2011. Uncertainty and predictability: the niches of migrants and nomads. In: Milner-Gulland EJ, Fryxell JM, Sinclair, ARE, editors. Animal Migrations: A Synthesis. Oxford University Press. p. 91-109.

Lea AM, Gray JT. 1935. The food of Australian birds: An analysis of the stomach contents. Emu. 35:63-98.

Mac Arthur RH. 1959. On the breeding distribution pattern of North American migrant birds. The Auk. 76:318-325.

McGoldrick JM, Mac Nally R. 1998. Impact of flowering on bird community dynamics in some central Victorian eucalypt forests. Ecol Res. 13:125-139.

Mettke-Hofmann C. 2007. Object exploration of garden and Sardinian warblers peaks in spring. Ethology. 113:174-182.

Mettke-Hofmann C, Gwinner E. 2003. Long-term memory for a life on the move. PNAS. 100:5863-5866.

Mettke-Hofmann C, Gwinner E. 2004. Differential assessment of environmental information in a migratory and a non-migratory passerine. Anim Behav. 68:1079-1086.

Mettke-Hofmann C, Lorentzen S, Schlicht E, Schneider J, Werner F. 2009. Spatial neophilia and neophobia in resident and migratory warblers (*Sylvia*). Ethology. 115:482-492.

Mettke-Hofmann C, Wink M, Winkler H, Leisler B. 2005. Exploration of environmental changes relates to lifestyle. Behav Ecol. 16:247-254.

Meyer AB, Wiglesworth LW. 1897. The Birds of the Celebes and the neighbouring Islands. Vol 1. Berlin: R. Friedländer.

Mönkkönen M, Helle P, Niemi GJ, Montgomery K. 1997. Heterospecific attraction affects community structure and migrant abundances in northern breeding bird communities. Can J Zool. 75:2077-2083.

Moore FR, Kerlinger P, Simons TR. 1990. Stopover on a Gulf coast barrier island by spring trans-gulf migrants. Wilson Bull. 102:487-500.

Powell SB, Paulus MP, Hartman DS, Godel T, Geyer MA. 2003. RO-10-5824 is a selective dopamine D4 receptor agonist that increases novel object exploration in C57 mice. Neuropharm. 44:473-481.

Pravosudov VV, Kitayski AS, Omanska A. 2006. The relationship between migratory behaviour, memory and the hippocampus: an intraspecific comparison. Proc R Soc Lond B. 273:2641-2649.

Prokopy RJ, Owens ED. 1978. Visual generalist with visual specialist phytophagous insects: Host selection behaviour and application to management. Entomologia Experimentalis et Applicata. 24:609-620.

Rand AL, Gillard ET. 1967. Handbook of New Guinea Birds. London: Weidenfeld and Nicholson.

Reed JM, Boulinier T, Danchin E, Oring LW. 1999. Informed dispersal: Prospecting by birds for breeding sites. Curr Orn. 15:189-259.

Reside AE, Van der Wal JJ, Kutt AS, Perkins GC. 2010. Weather, not climate, defines distributions of vagile bird species. PLoS One. 5:e13569.

Rival C, Olivier I, Ceyte H. 2003. Effects of temporal and/or spatial instructions on the speed-accuracy trade-off of pointing movements in children. Neurosci Lett. 336:65-69.

Sage RB, Robertson PA. 1996. Factors affecting songbird communities using new short rotation coppice habitats in spring. Bird Study. 43:201-213.

Sambrook J, Russell DW. 2001. Molecular cloning: a laboratory manual. New York: Cold Spring Harbor Laboratory Press.

Selonen V, Hanski IK. 2006. Habitat exploration and use in dispersing juvenile flying squirrels. J Anim Ecol. 75:1440-1449.

Sherry DF, Vaccarino AL. 1989. Hippocampus and memory for food caches in Black-capped chickadees. Behav Neurosci. 103:308-318.

Sol D, Lefebvre L, Rodriguez-Teijeiro JD. 2005. Brain size, innovative propensity, and migratory behaviour in temperate palaearctic birds. Proc R Soc Lond B. 272:1433-1441.

Tamura K, Peterson D, Peterson N, Steker G, Nei M, Kumar S. 2011. MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Mol Biol Evol. [Epub ahead of print]

Tebbich S, Fessl AE, Blomqvist D. 2009. Exploration and ecology in Darwin’s finches. Evol Ecol. 23:591-605.

Todt D, Hammerschmidt K, Hultsch H. 1992. The behavior of Barbary macaques (*Macaca sylvanus*): Perspective and projects of a long-term study. Primate Report. 32:19-30.

Troncoso JA, Vargas RR, Tapia DH, Olivares-Donoso R, Niemeyer HM. 2005. Host selection by the generalist aphid *Myzus persicae* (Hemiptera: Aphidae) and its subspecies specialized on tobacco, after being reared on the same host. Bull Entomol Res. 95:23-28.

Verbeek MEM, Drent PJ, Wiepkema PR. 1994. Consistent individual differences in early exploratory behaviour of male great tits. Anim Behav. 48:1113-1121.

Vince MA. 1960. Developmental changes in responsiveness in the Great Tit *Parus major.* Behaviour. 15:219-242.