

Exploration of environmental changes relates to lifestyle

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Decision making in informed animals is often described by optimality models. However, how information about an environment is acquired is rarely investigated. Cost/benefit considerations suggest that species differ in this respect according to their lifestyle. We tested the hypothesis that resident species react to changes in their familiar environment earlier and explore it more intensively than do nomadic species by observing the response to environmental changes (presentation of novel objects) in 10 parrot species. Phylogenetic relationships were taken into account. Residents touched the novel objects significantly earlier and explored more objects than did nomads. In addition, species with a high proportion of fruits in their food spectrum explored more than did species with other food preferences. The results are in accordance with different costs and benefits of information gathering for species that differ in their lifestyle and ecological demands. *Key words:* environmental assessment, neophilia, nomads, parrots, Psittacidae, residents. [*Behav Ecol*]

Information is the prerequisite for decision making. Optimality models based on the assumption that decision makers are fully informed often predict decisions of animals in a foraging or mating context quite well. Regardless of the currency involved (e.g., travel time, predation risk; Rodriguez et al., 2001; Scheiffarth et al., 2002; Zach, 1979; energy gain, mating rate, and others; Elnor and Hughes, 1978; Lin and Batzli, 2002), decision-making processes have been mainly investigated in situations in which an individual was familiar with its environment and hence informed about the distribution and quality of resources or mates. However, to acquire the appropriate knowledge, an individual must first assess its environment individually (Day et al., 1998; Göth and Proctor, 2002; Greenberg and Mettke-Hofmann, 2001; McMillan and Rothschild, 1994), by social learning (Altshuler and Nunn, 2001; Swaney et al., 2001; Visalberghi and Addessi, 2001) or by use of public information (Gros-Louis et al., 2003; Valone and Templeton, 2002). The exploring individual has to decide (1) which habitat or patch it should investigate, (2) in what detail it should explore it, and (3) which parameters of the environment it should assess and memorize. As most species live in changing environments, individuals must also decide how often they update their knowledge. Investigation of the environment not only is beneficial but also incurs costs (predation risk, energy expenditure, time). Thus, there should be a trade-off between the benefit (knowledge) and costs of environmental assessment (Mettke-Hofmann et al., 2002). Comparative studies show that bird species differ at least in some of the aforementioned aspects that can be explained by different ecological requirements and, hence, different costs and benefits of individual information gathering. For example, depending on the species' ecology, individuals approach

and investigate changes in their familiar environment (a novel object presented in the aviary) with different latencies and for variable duration (Mettke-Hofmann et al., 2002). The species' exploratory behavior was in concordance with hypotheses concerning the costs and benefits of exploration for the various species. Closely related food-storing and nonstoring bird species differ in the type of information retained—spatial or nonspatial (Brodbeck and Shettleworth, 1995; Clayton and Krebs, 1994). Thus, the process of environmental assessment can itself have a decisive influence on options in the future (File, 2001).

Inducing changes in the environment is a common way to investigate environmental assessment in animals, as they are often confronted with environmental changes in the field be it predictable (seasonally) or unpredictable owing to natural events or human activities. Species may deal differently with these environmental changes in order to meet their distinct requirements. Nomadism and site tenacity are two alternative reproductive tactics (Andersson, 1980) that require a quite different use of the environment. They may also relate to differences for reacting to changes in the environment. Nomadism is favored by a large interval between successive good years in an area and cyclic rather than random fluctuations, whereas residency is favored by seasonal environments (Andersson, 1980). Furthermore, individuals do better to change the territory when conditions get worse in unpredictable habitats with unequal territory qualities (Switzer, 1993). Nomadic species take advantage of temporary super-abundant food resources that are unpredictable in time and space (Brown and Hopkins, 1996; Dean, 1997; McGoldrick and Mac Nally, 1998). 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. If a nomad investigates small-scale environmental changes in its current staging site, the payoff might be relatively small, as new feeding opportunities will rarely

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Table 1
Test species

Tribe	Species	Sample size
Loriini	<i>Trichoglossus ornatus</i> (ornate lory)	7 (7)
	<i>Trichoglossus haematodus moluccanus</i> (rainbow lory)	7 (6)
	<i>Neopsittacus pullicauda</i> (emerald lorikeet)	7 (7)
	<i>Charmosyna josephinae</i> (Josephine's lory)	7 (6)
	<i>Charmosyna papou goliathina</i> (Papuan lory)	7 (7)
	<i>Charmosyna p. pulchella</i> (fairy lorikeet)	6 (5)
Platycercini	<i>Psephotus chrysopterygius dissimilis</i> (hooded parrot)	9 (8)
	<i>Psephotus varius</i> (mulga parrot)	7 (7)
	<i>Psephotus haematotus</i> (red-rumped parrot)	7 (7)
	<i>Northiella haematogaster</i> (blue bonnet)	8 (7)

Numbers in parentheses represent sample size (in pairs) in analysis.

emerge. As nomads leave the area when conditions get worse, they cannot use recently acquired information any longer, so that the costs may not be compensated by the benefits of exploration (Kerr and Feldman, 2003).

Residents, in contrast, select habitats for the long-term. They are more likely to be found in vegetation types that are stable throughout the year (e.g., coniferous vegetation; Airola and Barrett, 1985; Mac Arthur, 1959; Sage and Robertson, 1996). Residents rely on less rich but predictable food sources (Brown and Hopkins, 1996) in a relatively restricted area. Their food sources are predictable in the sense that they either are permanently available (even though not necessarily at the same location) or reoccur in a subannual or annual cycle (Brown and Hopkins, 1996). Thus, residents are challenged with changes in food type, abundance, and distribution across the year but less between years. For a resident, it may therefore be of paramount importance to be well informed about recent changes in food sources and food distribution as well as about competition, predation pressure, and forthcoming feeding opportunities. Because of the year-round residency, residents can use short-term as well as long-term information. Thus, we suggest that residents and nomads react differently to changes in their environment. More precisely, our hypothesis is that residents should react to changes in their familiar environment earlier and explore it more intensively than do nomads.

In this article we investigate how 10 parrot species (Psittacidae), belonging to two tribes that differ in their lifestyle—resident or nomadic—assess changes in their familiar environment. Within each tribe, species differed in their movement patterns (resident–nomadic). The tribes represented a nectarivorous/frugivorous group and a primarily seed-eating group, so that we could assess the relationship between a nomadic or resident lifestyle and exploratory behavior as a factor independent of feeding specializations. We tested our hypothesis by confronting the parrots with novel objects in their familiar aviary.

Exploratory behavior has a heritable component of about 54% (Drent et al., 2003). Therefore, possible differences in exploration are thought to have evolved as an adaptation to the species' lifestyle and/or its environmental conditions.

MATERIALS AND METHODS

Experimental birds

Experimental birds were 72 adult pairs belonging to 10 species (Table 1). 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 descendants 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 (Table 2). 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 (Bell, 1966; Coates, 1985; Forshaw, 1977, 1988; Meyer and Wigglesworth, 1897; Mettke-Hofmann C, personal observations) (Table 2). 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 (Boehm, 1959; Fleming, 1974; Forshaw, 1977, 1988; Lea and Gray, 1935; Mettke-Hofmann C, personal observations) (Table 2). The migratory behavior was assessed from the literature (Bell, 1982; Coates, 1985; Forshaw, 1988; Meyer and Wigglesworth, 1897; Rand and Gillard, 1967). Observation in the field (Mettke-Hofmann C, personal observations; Schodde R., personal communication) indicated that rainbow lorikeets (*Trichoglossus haematodus moluccanus*) are sedentary in the northern part of their range but become more and more nomadic toward the south. Mulga parrots (*Psephotus varius*) are sedentary in the center of their distribution and nomadic at its edges. Because origin could not be ascertained, both species were classified as resident as well as nomadic (Table 2).

Methods

Data collection occurred between May and August in three consecutive years. Pairs were kept in 2 × 2 × 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 called lory soup consisting of 35 g ground pollen, 50 g fruit sugar and honey, 30 g dry porridge, and 1 teaspoon yeast dissolved in 1 l water (Mettke-Hofmann et al., 1997). The Platycercini were kept with a mixture of seeds (sunflower, oats, conifer, chicory, thistle, lettuce, small millets, canary, and grass seeds). In addition, we offered half-ripe millet in ears. All birds had 10 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. Experiments started on day 11. Confrontation with the novel objects occurred for half of the pairs, equally distributed among the species, on days 11 and 14. The other half was first tested in a spatial exploration experiment on day 11 and subsequently confronted with the novel objects on days 15 and 18.

For the experiment, 1 h after food had been given at dawn, three novel objects—a rope, a cotton mop, and a set of three blue plastic tiles—were fixed with chains over a T-shaped perch. The distance separating each object from the others was 50 cm. The spatial relationship between the objects remained the same throughout all tests, but the location of the objects was rotated among the three positions within each species. Observation started with introduction of the objects and lasted for 6 h. The objects were removed next morning

Table 2
Ecological variables of the species

Species	R/N	ne	po	bl	fr	be	gs	ts	le	bu	in	hab	or
<i>Trichoglossus ornatus</i>	N	25	25	12.5	25	—	12.5	—	—	—	—	2	Sulawesi
<i>Trichoglossus haematodus</i>	R/N	25	25	3.6	25	3.6	3.6	3.6	3.6	3.6	3.6	3	Australia
<i>Neopsittacus pullicauda</i>	R	20	20	10	20	10	—	20	—	—	—	2	New Guinea
<i>Charmosyna josephinae</i>	N	25	25	6.2	25	—	—	6.2	—	6.2	6.2	2	New Guinea
<i>Charmosyna papou</i>	R	25	25	5	25	5	—	5	—	5	5	2	New Guinea
<i>Charmosyna pulchella</i>	N	25	25	12.5	25	—	—	—	—	—	12.5	2	New Guinea
<i>Psephotus chrysopterygius</i>	N	—	—	—	—	—	50	40	—	—	10	1	Australia
<i>Psephotus varius</i>	R/N	—	—	—	—	10	30	40	10	—	10	1	Australia
<i>Psephotus haematotus</i>	R	—	7.1	7.1	7.1	7.1	50	7.1	7.1	7.1	—	3	Australia
<i>Northiella haematogaster</i>	R	7.1	—	7.1	7.1	7.1	30	20	7.1	7.1	7.1	1	Australia

R/N indicates resident/nomadic; ne, nectar; po, pollen; bl, blossoms; fr, fruits; be, berries; gs, grass; seeds; ts, tree seeds; le, leaves; bu, buds; in, insects; and hab, habitat complexity (1, open woodland; 2, forest; 3, forest edge). Food types are given in approximate percentages according to their importance in the feeding spectrum of each species.

and presented again 2 days later for another 6 h. The position of each object was identical on both test days. To get a rough overview about the activity of each individual, the behavior of each bird and its location were recorded in 1-min-point sampling (Altmann, 1974). Continuous behavioral records, using a tape recorder, commenced when an animal approached the object closer than 30 cm.

Sample storage and DNA isolation

After the experiments were finished, blood samples were taken from the claw of one to eight individuals per species except for the Papuan lory (*Charmosyna papou*) and the emerald lorikeet to investigate the phylogenetic relationships of the birds. Blood samples were transferred into an APS buffer (0.1 M Tris at pH 7.4, 10% EDTA, 1% NaF, 0.1% thymol; Arctander, 1988). In addition, we collected livers of dead birds (others than our test birds) of all species. Overall, 49 samples were taken with a minimum of three per species and stored at -80°C until analysis.

Total DNA was extracted from the blood samples by an overnight incubation at 37°C in lysis buffer (10 mM Tris at pH 7.5, 25 mM EDTA, 75 mM NaCl, 1% SDS) including 1 mg proteinase K (Merck), followed by a standard phenol/chloroform protein extraction. DNA was precipitated from the supernatant with 0.8 volume of cold isopropanol, centrifuged, washed, dried, and resuspended in TE buffer.

Analyses

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

As a measure for exploration, we assessed (1) latencies between introduction of the objects and first tactile contact, (2) the number of objects touched, and (3) the duration of tactile exploration.

Phylogenetic relationships

Closely related species tend to behave more similarly than do less related species. Thus, species might not be statistically independent. To obtain independent data points, we incorporated phylogenetic relationships into our calculations. Phylogenetic relationships of most of the species tested were not available from published sources. Therefore, we determined phylogenetic relationships by comparing nucleotide sequences of the mitochondrial cytochrome b gene, which is a good marker for relationships within bird families (Broders

et al., 2003; Leisler et al., 1997; Wink, 1995; Wink and Heidrich, 1999).

PCR and sequencing

The mitochondrial cytochrome b gene was amplified by PCR using primers (L and H refer to light and heavy strands of mtDNA; numbers indicate the positions in the mt genome of *Gallus gallus*: MT-A3 (L-14995 within cyt b), GCC CCA TCC AAC ATC TCA GCA TGA TGA AAC TTC G; or mT-F2 (H-16065 within tRNA thr), CTA AGA AGG GTG GAG TCT TCA GTT TTT GGT TTA CAA GAC CAA TG. PCR was performed in 50 μl volume containing 1 unit of Amersham Pharmacia Biotech *Taq* DNA polymerase, 50 mM KCl, 1.5 mM MgCl_2 , and 10 mM Tris-HCl (pH 9). After an initial denaturing step for 5 min at 94°C , 31 cycles were performed with annealing 52 s at 60°C , primer extension 80 s at 72°C , and denaturing 45 s at 94°C .

PCR products were sequenced directly by using the dideoxy chain termination method with the cycle sequencing Kit (Amersham Life Science, RPN 2438/RPN 2538) in combination with internal CY-5 labeled primers (1.5 pmole). For cycle sequencing, a two-stage program comprising an initial denaturing step for 4 min at 94°C and 25 cycles at 60°C (40 sec) and 94° (30 sec) was used. The primers used were as follows: mT-C2-CY(L-15298), XGA GGA CAA ATA TCA TTC TGA GG; mT-C6-CY (H-15649), XGCT GGR GTR AAR TTT TCT GG; or mT-le-cy (L-15697), XTCA AAC CCG AAT GAT AYT TCC TAT T. CY-5-labeled fragments were analyzed on an automated DNA sequencer (Amersham Pharmacia Biotech, ALF-Express II).

Alternatively, a cycle sequencing reaction (final volume = 10 μl) was carried out after the initial PCR. Reaction buffer consisted of 2 μl reaction mix with BigDye terminators (according to the BigDye Terminator Protocol; ABI Applied Biosystems), 10 pmole primer (smtA, 5'-CAA CAT CTC AGC ATG ATG AAA CTT CG-3' and mtC, 5'-TAY GTC CTA CCA TGA GGA CAA ATA TCA TTC TGA GG-3'). The cycle sequencing was carried out in 25 cycles for 10 s at 96°C , 5 s at 52°C , and 4 min at 60°C . Sequencing products were purified by precipitation: 1 volume reaction mix, 1/10 3 M NaAcetate (pH 4.6), and 2.5 volume ethanol. After centrifugation for 15 min at 13,000 rpm, DNA pellets were washed in 70% ethanol and taken up in 20 μl distilled water. The purified DNA was diluted 1:5 in water and applied to a 16-column automatic capillary sequencer (ABI 3100) by using 50-cm capillaries and POP6 as a polymer.

Sequences of 1143 nucleotides were obtained directly from the sequencer and aligned. No deletions, insertions, or

inversions were encountered. Various PCR primers generated only a single product. Because no stop codons were found and because nucleotide abundance corresponded to those of mtDNA, we conclude that we have amplified and sequenced mtDNA and not nuclear copies of mitochondrial genes.

Phylogenetic and statistical analysis

The data were analyzed by using maximum parsimony (MP) and maximum likelihood (ML) with PAUP* 4.0b10 (Swofford, 2002). Genetic distances (uncorrected p -distances) were calculated from a data set of 1143 bp. Unweighted MP analyses were performed by using tree-bisection-and-reconnection (TBR) branch swapping and the heuristic search option. ML has proven to be powerful and is now widely applied (Huelsenbeck and Crandall, 1997). ML trees were reconstructed by using TBR branch swapping and the heuristic search option but with estimates of nucleotide substitutions, invariant sites, and γ parameters initially calculated from a neighbor joining (NJ) tree. A molecular clock was not enforced. Distribution of rates at variable sites = γ (discrete approximation; shape parameter $\alpha = 0.5$; number of rate categories = 4; representation of average rate for each category = mean). These settings correspond to the GTR + G model.

Interspecific comparison

The two birds within each pair might influence each other's decision to explore the novel objects. Therefore, means of the exploration values from both partners were used for all calculations.

For the interspecific comparison, exploration variables were related to the migratory behavior of the species (nomadic/resident) and eight ecological variables. We divided migratory behavior into three categories: nomadic, nomadic/resident (species includes resident as well as nomadic populations), and resident. We included eight ecological variables, which may also be responsible for exploration differences (see Mettke-Hofmann et al., 2002). Seven of these described different food types. The seven food types were selected out of 10 possible food types used by the species (Table 2). Correlation analyses showed that nectar, pollen, and fruits were highly correlated with each other, as were berries with migratory behavior. Thus, we included only fruits from the former and migratory behavior from the latter set of variables. We assigned approximate percentages to food types according to their importance in the feeding spectrum of each species. The eighth ecological variable coded the habitat type with respect to its complexity. Altogether three categories of habitat types were used by the species (Table 2). Open woodland was categorized as simple habitat, whereas forest edge was on the other end as a highly complex habitat with a variety of strata levels. The complexity of forests is intermediate (see Mettke-Hofmann et al., 2002). Species inhabiting several habitat types were assigned the value corresponding to the type predominantly used.

For the comparison of latencies, a further variable was included. Latencies until an object is touched can be a function of how interested an individual is in changes in its environment. However, differences in latencies can also be caused by different activity levels. Thus, we included activity as a further independent variable. Within the first hour after introduction of the objects, we counted each change in location for each bird separately and calculated the mean of both birds in a pair in each species, which was used for analysis ($N = 10$).

Analyses were twofold: first, we used species as independent data points in multiple regression analyses; second, we considered phylogenetic relationships among the species by use of phylogenetic generalized least-squares regressions (PGLSR).

In the first analysis, multiple regression analyses were based on an exhaustive search through all possible combinations of maximally three predictors, so that we avoided problems associated with stepping methods. To avoid overfitting of the model, we restrained multivariate analysis to three variables, although the widely used Akaike information criterion (Akaike, 1974) suggested to include more predictors. A regression analysis was used for each dependent variable (latency, number of objects touched, duration of exploration) with nine (10 for the latencies) independent variables. The PGLS regression analyses were confined to the three variables selected in the multiple regression analyses. For the comparative analyses, we used generalized linear methods (Dobson, 1990). Models of this kind can be extended to include covariances among species owing to the evolutionary process (Martins and Hansen, 1997; Rohlf, 2001). Thus, the full range and power of this tool are available for statistical analyses in comparative studies, without the problems that pertain to popular algorithmic methods (e.g., independent contrasts)—although the latter can give identical results under certain boundary conditions (Garland et al., 1999; Price, 1997; Rohlf, 2001). We assumed a normal distribution for the dependent variable and an evolutionary change that follows a Brownian-motion model (Felsenstein, 1985). To produce normally distributed variables, latencies and duration of exploration were transformed with LG(10) and the number of objects touched with square-root. Percentages (food categories) were transformed with the square-root-arcsine transform.

Housing conditions and experiments were in accordance with German institutional guidelines and legal requirements. All birds had valid CITES certifications. (Convention on International Trade in Endangered Species of Wild Fauna and Flora).

RESULTS

Phylogenetic relationships

Phylogenetic relationships were reconstructed by using character and distance methods. ML, MP, and NJ produced trees with almost identical topologies (Figure 1).

Psephotus and *Northiella* cluster as a monophyletic group (99% bootstrap support) that is basal to the clades comprising two sister groups (92% bootstrap support) with *Charmosyna* (99% bootstrap support) and *Trichoglossus/Neopsittacus* (100% bootstrap support). We considered the ML tree a reliable framework for the comparative analyses.

Residency and nomadism did not cluster in a specific section of the tree (Figure 1 and Table 2). Considering residency as the ancestral state for the Order Psittaciformes, nomadism seems to have evolved three times independently in the clades *Charmosyna*, *Psephotus/Northiella*, and *Neopsittacus/Trichoglossus*, suggesting that these traits evolved as an adaptation to the particular conditions a species has been exposed to.

Interspecific comparison

Analyses with species as independent data points

First, latencies until the first touch of an object were related to differences in migratory behavior (resident-nomadic) (Table 3). Nomadic species had longer latencies than did resident species. In addition, the variable "fruits" showed a relationship to exploration latencies. Species with a high proportion of fruits in their food spectrum explored earlier than did those in which fruits played a minor role (Table 3). Overall, these variables explained 83% of the variance (multiple regression, $F_{2,7} = 17.117$, $p < .005$).

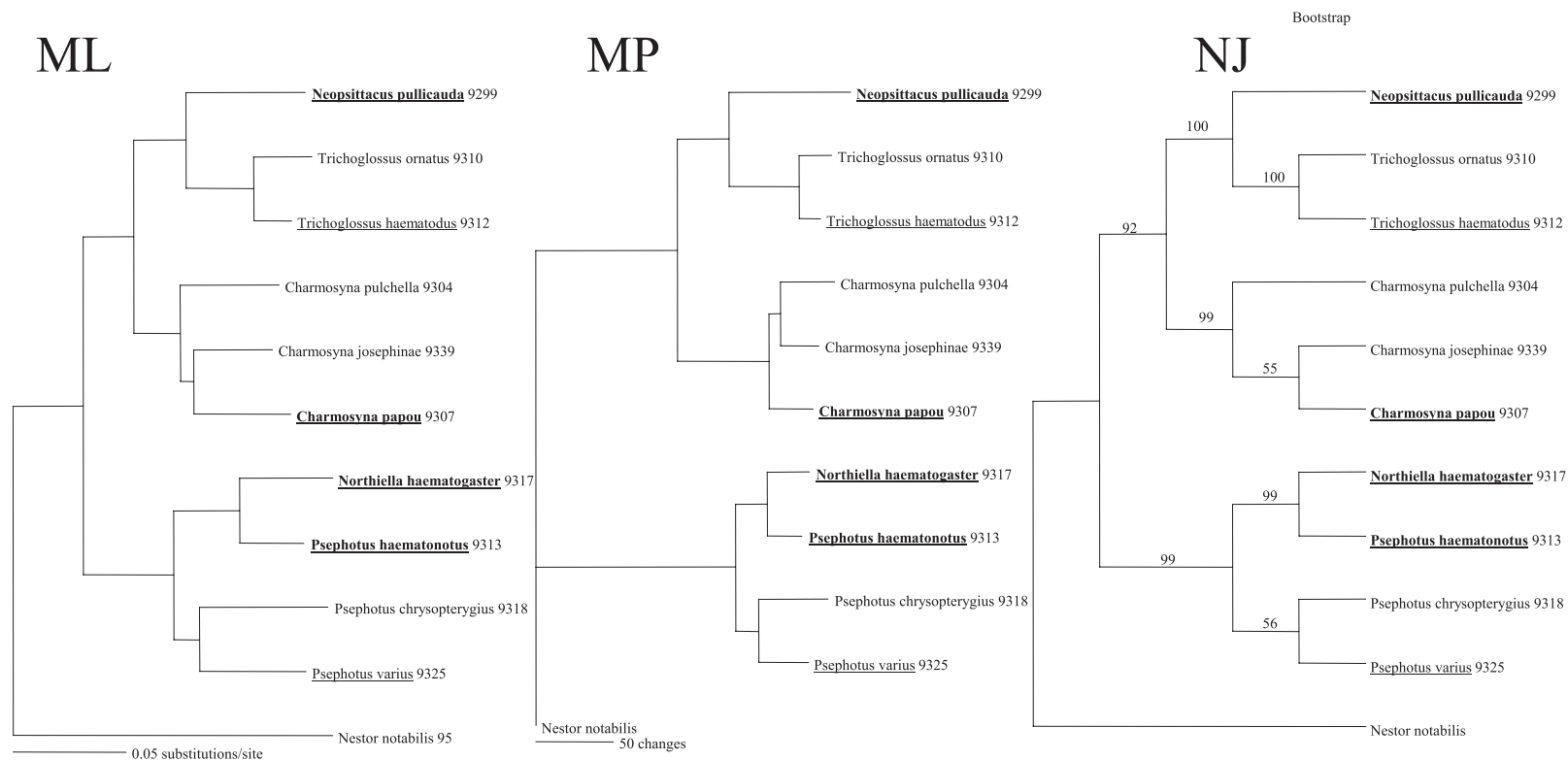


Figure 1
 Phylogenetic relationships of the species. Phylogeny reconstruction by ML, MP, and NJ; numbers at branches refer to bootstrap values from 1000 replications. Bold and underlined indicates resident; underlined, resident/nomadic; and rest, nomadic

Table 3
Association of ecological variables and migratory behavior with exploration

Variable	Latency		No. of objects touched	
	<i>T</i> value	<i>p</i>	<i>T</i> value	<i>p</i>
R/N	-3.742*	0.009	2.856	0.028
Fruits	-3.683	0.010	4.599	0.003
Activity	-2.068	ns	—	—
Leaves	—	—	2.745	0.033

Relationships between exploratory behavior (latency, number of objects touched) and ecological variables as well as migratory behavior are shown. R/N indicates resident or nomadic; NS, not significant.

* Values are only given for the three variables selected in the model (see text).

The number of objects touched was again related to the migratory behavior. Residents touched, on average, more objects than did nomads. Furthermore, fruits and leaves were significantly associated with the number of objects touched (multiple regression, $r^2 = .882$, $F_{3,6} = 15.015$, $p < .005$) (Table 3). The higher the proportion of fruits and/or leaves in the diet, the more objects were touched.

Duration of exploration was not related to a resident or nomadic lifestyle but to the proportion of fruits, buds, and leaves in the diet (multiple regression, $r^2 = .736$, $F_{3,6} = 5.5887$, $p < .05$).

Analyses of phylogenetically independent data points

Inclusion of phylogenetic dependencies did not change the results much. The relationship between latencies to touching the objects and a resident or nomadic lifestyle (Figure 2) as well as the association between fruits and exploration latencies remained significant. A resident or nomadic lifestyle alone explained 44% of the variance (PGLSR, $F_{1,8} = 6.1753$, $p < .05$). Overall, 87% of the variance were explained by the two variables (PGLSR, $F_{3,6} = 13.6034$, $p < .01$). All three variables influencing the number of objects touched remained significant under consideration of phylogenetic relationships (PGLSR, $r^2 = .875$, $F_{3,6} = 14.0261$, $p < .005$). Again, a resident

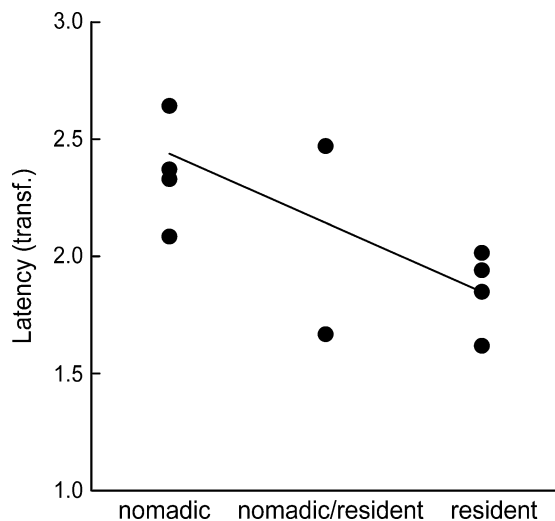


Figure 2
Relationship between exploration latencies and a resident or nomadic lifestyle. Species means of exploration latencies (transformed) are plotted against the migratory behavior of the species. Regression line represents the results of a PGLSR.

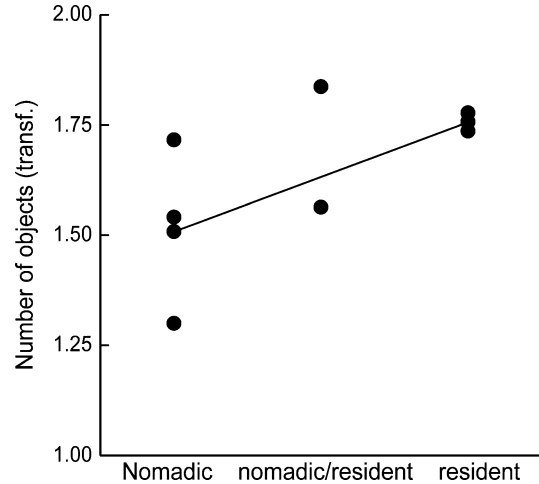


Figure 3
Relationship between the number of objects touched and a resident or nomadic lifestyle. Species means of the number of objects touched are plotted against the migratory behavior of the species. Regression line represents the result of a PGLSR.

or nomadic lifestyle alone explained 45% of the variance (PGLSR: $F_{1,8} = 6.6492$, $p < .05$) (Figure 3). However, we could not corroborate the significant relationship between duration of exploration and the food variables when we accounted for phylogenetic dependencies (PGLSR, $F_{3,6} = 4.4916$, $p = ns$).

DISCUSSION

The present study aimed to test the hypothesis that resident bird species react sooner to changes in their familiar environment and explore them more than nomadic species do, by comparing 10 closely related parrot species which differed in their migratory behavior.

Phylogeny

The phylogenetic analysis showed that among the 10 species under investigation, nomadism and residency were independent of phylogenetic relationships: even within closely related sister taxa, one species can be nomadic and another one resident. The phylogenetic results thus clearly show that the ecological traits evolved without phylogenetic constraints (Figure 1 and Table 2).

Interspecific comparison

The interspecific comparison revealed that the species differed in their reaction to changes in the familiar environment. As hypothesized, residents touched the objects significantly earlier and investigated more objects than did nomads (Table 3 and Figures 2 and 3). This relationship was evident both with and without taking phylogenetic relationships into account. The relationship to other ecological variables, however, showed at least some phylogenetic bias. We will, therefore, concentrate the discussion on the results obtained from the phylogenetically controlled analyses.

Nomads and residents use resources that differ strongly in their predictability in time and space and their abundance at a given time. Related to this, movement patterns and habitat use of nomads and residents are quite different in terms of temporal and spatial dimensions. The different use of resources and movement patterns seems to be accompanied

by specific information-processing strategies. For a resident, which lives permanently in a particular habitat and which has to deal with environmental changes, a rapid assessment of the environment is important to discover changes early in time. Changes can signal newly emerging feeding opportunities, and an early discovery is advantageous to get access to new food first. Moreover, discovery of novel food patches helps to overcome periods of food shortage. Also, a detailed knowledge of the environment at any given time allows to adapt the behavior to local conditions which can be crucial for future breeding success or winter survival. In addition, ripening processes in plants lead to highly predictable results. Through exploration, birds may discover early stages of such processes (e.g., flower buds), which is highly valuable because it gives information about forthcoming feeding opportunities and hence influences decision making. Learning theories predict that it pays to investigate reliable stimuli to optimize behavior (Kerr and Feldman, 2003). Exploratory behavior is closely linked to the concept of latent learning in that the information gathered in this way may be used much later (Nitta et al., 1996; Renner, 1988). Changes in the environment are related not only to the feeding context but also to other contexts. For instance, availability and suitability of nesting trees and cavities change over time. Discovery of a new and better nesting tree will increase reproductive success. Thus, a rapid and detailed investigation of changes in the environment is beneficial for a resident bird.

Nomads, in contrast, often change their place of living and use short-term available resources that do not renew in a period of time that makes a stay reasonable. Thus, investigation of changes in the environment will rarely result in the discovery of new feeding opportunities. In addition, nomads leave the area when conditions deteriorate and recently acquired information cannot be used any longer. In nomads, the costs of a rapid and detailed investigation of environmental changes might, therefore, exceed benefits (Kerr and Feldman, 2003). Instead of investing time in small-scale exploration of environmental changes in familiar areas, nomads might invest more in large-scale spatial exploration outside the familiar environment to follow the course of flowering and fruiting plants.

Exploration latencies and the number of objects touched were further associated with the degree to which species feed on fruits (Table 3). In most cases, fruits remained in the analyses even after consideration of the phylogeny, which indicates a phylogenetically independent relationship between fruits and exploration patterns. This is consistent with earlier findings: a large proportion of fruits in the food spectrum facilitates exploration (Mettke-Hofmann et al., 2002). Fruiting plants are separated in time and space and, hence, represent a highly variable food source. McNamara and Houston (1985) illustrated that information is most useful when the source is highly variable. Changes in the environment can signal new flowering or fruiting plants. Thus, exploring changes can be highly beneficial for an individual that depends on variable food sources.

To summarize, the reaction to changes in the familiar environment varied with the lifestyle of a species. A resident lifestyle requires a rapid update of environmental changes, whereas a nomadic lifestyle does not. This may be owing to a long- versus short-term use of a particular habitat in residents and nomads. The reaction to changes was also related to other factors (e.g., food type).

The results presented here deal with reaction to changes in the familiar environment. However, residents and nomads are also differently confronted with novel environments. Further studies will investigate how differences in migratory behavior and reaction to novel environments are related.

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