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Individuality in the Northern Bald Ibis or Waldrapp Ibis *Geronticus eremita* – key features for a complex social system

Individualnost klavžarja *Geronticus eremita* - poglavitne značilnosti zapletene socialne strukture teh ptic

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The authors of the article studied some factors of individual distinctiveness in the Northern Bald Ibis or Waldrapp Ibis *Geronticus eremita*. Grey head patterns are the most striking optical signs showing individual differences. Beside visual signals, acoustic communication shows a high intraspecific variation. A thorough analysis of the "*croop*"-call reveals strong evidence for age, sexual and individual variation. In addition, the variation within one type of vocalization may transmit various messages about the motivational state of the signaller.

Key words: Northern Bald Ibis, Waldrapp, *Geronticus eremita*, individual recognition, behaviour

Ključne besede: klavžar, *Geronticus eremita*, osebnostna razpoznava, vedenje

1. Introduction

The communication system of the Waldrapp Ibis *Geronticus eremita* consists of visual and auditory displays. The highly social species utters few vocalization types in many different contexts (Thaler *et al.* 1981, Pegoraro 1992, 1996, Pegoraro & Föger 1995). Analyses of vocal sequences may improve our understanding of mechanisms for maintaining social structures within and between colonies. Within breeding groups, specific individual behaviour patterns should exist. In particular, optical and/or acoustic cues for recognition of breeding partners and other group members are necessary for undisturbed reproduction (Saunders 1983). In Waldrapp Ibises the dark grey patterns on the naked heads are the most important optical cues (Pegoraro & Malin 1990).

In this paper we discuss results of the long-term studies concerning the importance of individual distinctiveness. Some functions of the birds´ calls for social behaviour, acoustic distinctiveness and individual recognition are presented. Additionally, optical features are documented and the potential of further investigations is discussed.

2. Methods

2.1. The study populations

The results derive mainly from ten years of intensive observations of the Waldrapp Ibis colony of the Alpenzoo Innsbruck (Tyrol/Austria). All individuals of this breeding group are of Moroccan origin. Further studies in aviaries were done in different zoological gardens in Switzerland and in Bireçik, SE-Turkey. Additional work was undertaken in the field in Bireçik (1984) and in Morocco (1986 – 1994).

2.2. Head patterns

Between 1984 and 1999, the head markings of 24 birds of the Alpenzoo colony were continuously documented. Photographs of each individual were taken at least once a year to establish a detailed cartography of the patterns. With this database it was possible to analyse the importance of this feature for individual distinctiveness as well as constancy over the study period. Additional pictures originate from Zurich Zoo, Switzerland and Bireçik, Turkey.

2.3. Recording and analysing techniques of vocal signals

The vocal inventory of twelve individuals was recorded at the Alpenzoo Innsbruck during a four-year observation period. Additional records were taken at the Zurich Zoo. The calls were recorded using a Nagra III tape recorder (tape speed: 19 cm/s) and a Grampian DP4/X microphone attached to a 60 cm parabolic reflector. Sonagrams of 1400 recordings of good quality were made at the Max-Planck-Institut für Verhaltensphysiologie, Vogelwarte Radolfzell at Radolfzell-Möggingen, Germany on a Kay Elemetrics sonagraph 6061 B with a filter width of 300 Hz (wide) at a frequency range of 80 to 8000 Hz, linear scale. Sonagrams were overlaid with a transparent grid to measure twelve parameters. These parameters were selected according to Bailey & Baker 1982, McGregor & Krebs 1982, Sparling 1983 and Zann 1984. The measurements of frequency and time parameters allowed an accuracy of 0.5 mm (1 mm = 83.3 Hz, 1 mm = 8.2 ms).

2.4. Statistical analysis of vocal signals

The measurements of nine acoustic parameters of the „*croop*"-call were used for the statistical analyses (see Pegoraro & Föger 1995). We used ANOVA to test for differences between individuals, sexes, age groups and calls uttered in two different social contexts – greeting and threat behaviour. Stepwise discriminate analysis was used to examine which variables are most important to discriminate individual calls (Fletcher *et al.* 1978, Smith *et al.* 1982). This multivariate procedure allows the elimination of unimportant variables using Wilks' Lambda and F-value to determine significance levels. Discriminant analysis was used to calculate a similarity matrix of the individual calls´ mean values, which were assigned to the most probable bird calling. A description of further criteria, advantages and disadvantages of statistical methods used here and their application in sonagram analysis are given by Lachenbruch (1975), Sparling & Williams (1978) and Martindale (1980).

3. Results

3.1. Head patterns

The dark head patterns of Waldrapp Ibises do not exist in first-year juveniles. During the first year the head is covered with a short and dense plumage of grey feathers with white edges. The neck-ruff is hardly developed at this age. The head remains at least partly feathered throughout the second year of life. The timing of the loss of these feathers differs individually. On bare parts of skin the dark head pattern appears simultaneously. The principal pattern of the head markings is now recognizable (e.g. degree of darkness or brightness) and begins to develop.

When fully developed, these markings are individually different (Figure 1). Some heads are very bright nearly lacking darker parts, others are almost completely black. All transitions between these extremes are possible. Like in other species (e.g. Bateson 1977) even a human observer is able to distinguish the birds individually with the help of these optical features (Pegoraro 1996). The presentation

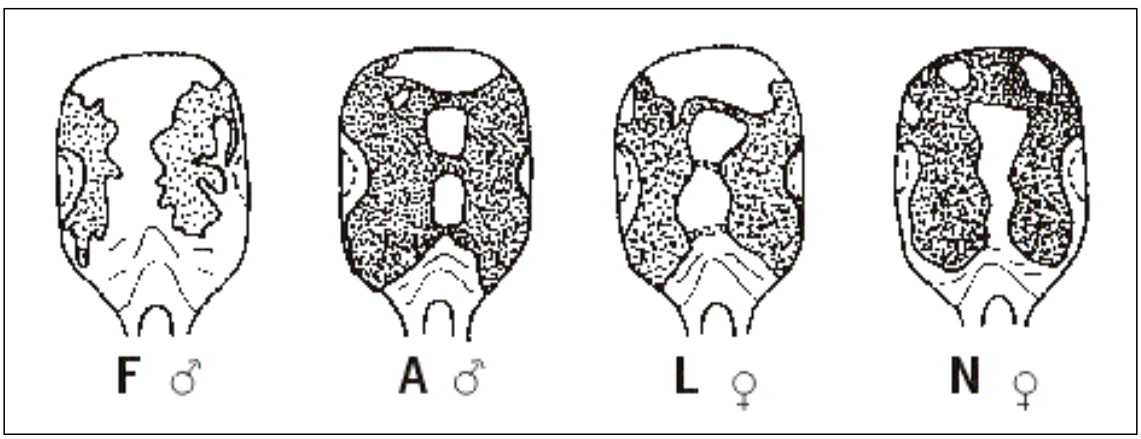

Figure 1: Four different head markings of adult Waldrapp Ibises

Slika 1: Štirje različni klavžarjevi naglavni vzorci

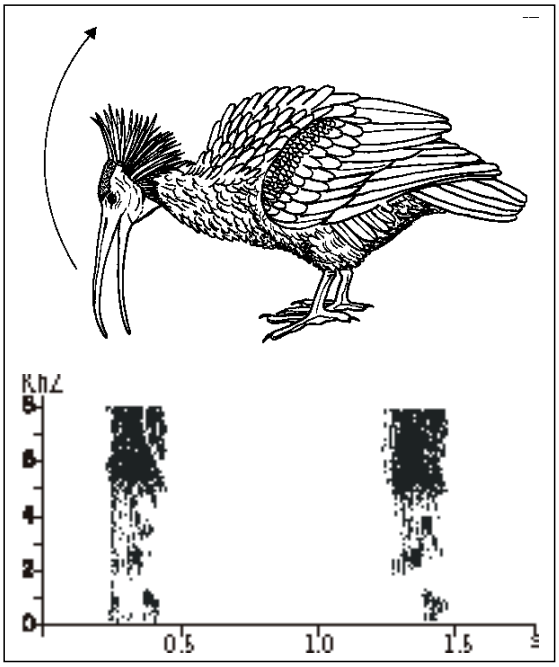

Figure 2: Greeting posture and sonagram of typical "*croop*"-calls uttered in this context

Slika 2: Pozdravna drža in sonogram tipičnega "*krupovskega*" oglašanja v tem kontekstu

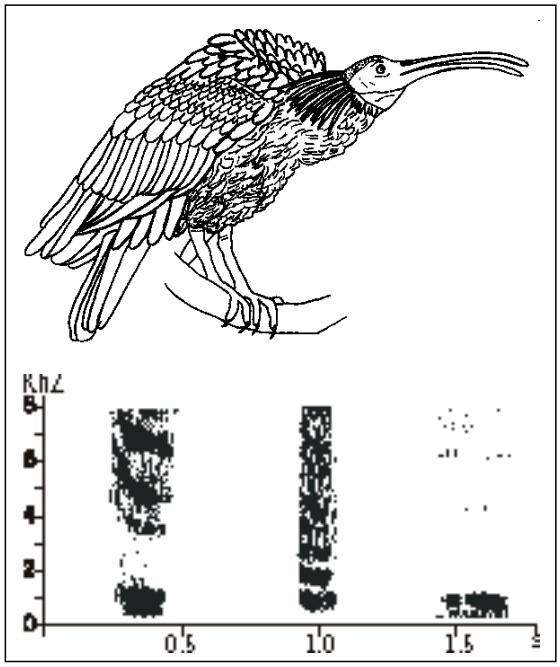

Figure 3: Excitation posture and sonogram of „*groo*"-calls uttered in this context

Slika 3: Drža razburjene ptice in sonogramam "*grumovskega*" oglašanja v tem kontekstu

of these markings to conspecifics is an important part of the typical greeting ceremony of Waldrapp Ibises (see Figure 2). Graphical comparisons indicate that head patterns may be inherited as parents and their offspring show similar primary patterns. To obtain more information on this question, further investigations using statistical analyses are needed. Another question we are currently studying is, if additional messages for conspecifics (e.g. fitness parameters) are also transmitted with the head markings.

3.2. Acoustic signals

The vocal inventory of the Waldrapp Ibis consists mainly of simple calls. As it is often the case in social bird species (Nottebohm 1975), they have a rather small repertoire of vocalizations. Adult birds use just three main types of calls, which can generally be derived from the vocalizations of juvenile birds. When artificially incubated and hand-reared (isolated from adult conspecifics), the ibises develop normal vocalizations (Pegoraro & Thaler 1993). This finding is contradictory to learning of calls by tradition; their patterns must be to a high degree genetically determined (Konishi 1963). In addition, instrumental bill noises occur. All acoustic signals are performed by both sexes and all vocalizations, except the excitation call, are used more often by males than females.

During pair contacts the birds produce a sort of "grumbling", composed of one to several short syllables with strong frequency and amplitude modulation. The monosyllabic "*groo*" represents an unspecific excitation call (Figure 3). It consists of one to three elements. In most cases the basic frequency range is dominant and the frequencies between 1200 and 3500 Hz are often missing. Although these calls show high intraindividual variation they are highly individual according to different features (e.g. mean frequency range, modulation and number of frequency bands).

A thorough analysis was done for the most frequent vocalization of Waldrapp Ibises, the monosyllabic "*croop*"-call (Pegoraro & Föger 1995). It consists of several elements. Its mean duration is 180.08 ms (± 58.03; n = 289) in male and 168.93 ms (± 87.13; n = 101) in female. In most cases it rises rapidly, followed by a slower decline (Figure 2).

Frequency bands of single elements usually decline, rarely increase and are shaped like a bar, banner, roof, arch, wave, or a flattened, sometimes inverted V or U. Considerable rhythmic frequency modulation often causes a scratched appearance to the sonagram.

As it has been demonstrated in calls of other nonpasserine birds (e.g. Sparling 1983, Bretagnolle 1989), the Waldrapp Ibises' "*croop*"-calls are uttered in the coarse of different displays and in different social contexts (Pegoraro 1996). They accompany greeting ceremonies as well as threat displays, respectively. During greeting, nest advertisement and copulation "*croop*"-calls are repeated. Greeting and threat displays have been described by many authors (e.g. Wackernagel 1964, Bauer & Glutz von Blotzheim 1966, Cramp & Simmons 1977, Hirsch 1979, Oliver *et al.* 1979, Thaler et al. 1981, Sahin 1983A, 1983B, Pegoraro & Thaler 1985, Sahin 1990). The results of an ANOVA analysis show that only duration differs significantly between these social contexts (F-value = 3.92, $p < 0.05$). On average threat calls last 24.6 ms longer than during greeting. The birds greet during pair, family as well as group contacts. The latter displays are characterized by sweeping head movements and very loud vocalizations allowing communication over long distances. Pair partners greet each other during any approach, nest relief, allopreening and presentation of nesting material. The function of calls uttered in these contexts are the synchronization and bonding of the breeding partners (Pegoraro & Thaler 1985). For analyses of individuality of "*croop*"-calls, only greeting calls were used for further computation.

Male and female calls are clearly distinguishable. The analysed parameters, except for two, proved to be significant. 81.6 % of the calls were classified correctly by discriminant analysis. ANOVA results showed differences in all parameters between two young females and ten adult individuals (including adult females). Minimum frequency range and mean frequency range of young birds are lower than those of older females. These characteristics are actually typical of adult males. On average the duration of the calls of young females is longer than those of older Waldrapp Ibises of both sexes. The higher value of duration coincides with greeting movements which appear exaggerated. The number of frequency bands visible in sonagrams is higher, corresponding to the loudness the calls on the one hand and the shape of frequency bands on the other.

A first simple subjective indication for the individuality of the vocal repertoire is the possibility of discriminating of calling individuals by humans. We were able to recognize the greeting calls of different individuals (see Saunders & Wooller 1988). For example, one individual sounded very quiet, low in frequency, often "croaking"; the calls of another bird were remarkable for their loudness, clipped manner and abrupt ending. The same characteristics are detectable in the sonagrams. For control, an independent person was asked to sort 38 sonagrams from six individuals selected at random according to their similarity: 36 of these were assigned correctly.

Calling the partner to the nest over of long distances could also indicate individual recognition by voice. However, this might only be a case of acoustic or optic nest locating (Tschanz 1968). Furthermore, in the case of visual contact, optical features of the partners might be involved.

The results of playback experiments with fledglings vs. parents provide further indications for individual recognition (cf. Pegoraro & Föger 1995). Young birds showed - except in two cases - strong reactions only to playbacks of the calls of their own parents ($n = 48$).

On the basis of this results we performed multivariate analysis of our data to examine all important parameters and their possible significance for individual recognition. The ANOVAs for each variable reveal highly significant interindividual differences, four acoustic features providing the best cues for individual recognition (Pegoraro & Föger 1995). Using these four variables, a high percentage (up to 86 %) of the Waldrapp Ibises in our sample could be identified correctly. This proportion is very similar to those reported for other nonpasserine birds (e.g. Beightol & Samuel 1973, Eakle *et al.* 1989).

4. Discussion and conclusions

4.1. Optical distinctiveness

The most apparent optical features of adult Waldrapp Ibises are their grey head markings. As they are presented to conspecifics during different social displays, there should be some message in these markings. On the one hand they could serve as a cue or signal for individual recognition. On the other hand they possibly include further information (e.g. fitness, family membership) playing an important role in sexual selection (Møller 1993).

Additionally, other morphological features could be involved in the visual identification system of the species. Some body measurements, such as the length of the tarsometatarsus and body diameter, vary considerably between individuals and allow

an experienced human observer to discriminate between some birds without seeing further features. A combination of the shape of the head, mimics and the distribution of skin wrinkles on the bare parts of the head is also useful for individual recognition as it is the case of human face recognition.

4.2. Function of calls

The paucity of vocal signals does not necessarily mean that social interactions are rare (Nottebohm 1975). The vocal inventory of the highly social Waldrapp Ibis consists of only few calls. Within each type of calls there is a certain range of variation to each call within one specific individual's repertoire, and each variation may convey different information according to the motivation of the bird and its social situation. The potential number of information which could be transmitted with a specific system of signals in general exceeds the number of signals. The situation during calling, the identity of the calling individual and the reaction to the signal by other members of the group allow conclusions regarding the function of the vocalization. It is possible that differing structures of certain frequency bands of the calls contain information about the emotional and physiological state of the bird, its intention for action and/or the type of relationship among group members (Zahavi 1982, Armstrong 1992, Pegoraro & Föger 1995). Additionally mixed calls and transitional forms of calls increase the possibility of transmition of different messages with this specific signal.

Waldrapp Ibises utter "*croop*"-calls during greeting ceremonies as well as threat displays. Although some transitions may be included, statistical analysis allows easy discrimination between the acoustic structure of the calls used in these differing contexts. So two types of "*croop*"-calls exist in the species. A similar differentiation seems to be reliable for other calls.

Waldrapp Ibises show no sexual dimorphism in morphology neither very striking differences in behaviour or patterns between sexes. Hence the sex of an individual could be encoded in its vocalizations. Our results support the hypothesis that the calls uttered during greeting ceremonies may serve for sexual recognition.

Furthermore, greeting calls provide information on the age of the calling individual. This seems to be important in the case of young birds breeding for the first time. As young ibises show rather clumsy courtship behaviour (Pegoraro & Thaler 1985), it could be of advantage for them to be recognizable as inexperienced birds. The "normal" reaction of older birds to such behaviour is aggression. Recognizing of the young age of a potential partner may appease the older, experienced birds. Up to the end of the second year of life the feathering of the head of Waldrapp Ibises decreases gradually (Pegoraro & Malin 1990). In the third year, when they reach sexual maturity, they are no longer sufficiently characterized by optical cues. For this reason it could be important that acoustic features prevent the delay of pair formation. Group-living in birds is generally associated with strong selection pressure for individual recognition (Falls 1982). If members of a group know each other, costly agonistic behaviour can be minimized. Additionally, acoustic individual recognition may function as an isolating mechanism for breeding partners against neighbours. The multivariate analyses of adult Waldrapp Ibis, greeting calls using nine frequency and temporal parameters indicate that these parameters form a suitable acoustic bases for individual recognition. The statistical analyses have shown that, in spite of high intra-individual variability, the calls of individual birds are relatively constant and that some special features of calls do not change individually. Frequency parameters associated with amplitude as well as phase parameters lead to a very complex pattern very likely to be a source of great variability. Multiple features may be involved in individual recognition, and if some are missing or masked, others may partially compensate for the loss (Robisson 1990). The parameters included in our analyses, as in many others (e.g. Goldstein 1978, Sparling & Williams 1978, Martindale 1980, Smith *et al.* 1982, Lequette & Jouventin 1991), are not able to describe all characteristics of vocal signals. The sonagrams' shapes of single individuals vary considerably. Therefore we suppose that shape includes additional information, but this remains to be tested. For this purpose, besides qualitative methods, statistical analysing techniques to minimize observer bias, like the experiments and procedures suggested by Chabot (1988), are necessary.

Although the greeting call allows the identification of individuals, it should be taken into consideration that the whole repertoire of a single bird might share a specific common quality, like in human voices (Weary *et al.* 1990). So for individual recognition, Waldrapp Ibises could be able to learn individual voice characteristics and use them to classify all vocal signals of adult conspecifics.

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5. Povzetek

Avtorja članka sta preučevala nekatere faktorje individualnih značilnosti klavžarja *Geronticus eremita*.
Sivi vzorci na goli glavi so najizrazitejša optična znamenja, ki govorijo o individualnih razlikah pri teh pticah. Klavžarjeva akustična komunikacija kaže, poleg vizualnih znamenj, na velike razlike med posamezniki. Temeljita analiza njegovega oglašanja (*"krup"*) razodeva njegovo starost, spol in druge osebnostne razlike. Poleg tega lahko razlike znotraj enega tipa vokalizacije dajejo različna sporočila o njegovem motivacijskem stanju.

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