

FORM AND FUNCTION OF AERIAL COURTSHIP DISPLAYS IN BLACK STORKS *Ciconia nigra*

Oblika in funkcija dvorjenja črnih štokelj *Ciconia nigra* v zraku

PETER SACKL

Steiermärkisches Landesmuseum Joanneum, Forschungsstätte Furtnersteich, Raubergasse 10, A-8010 Graz, Austria
e-mail: peter.sackl@stmk.gv.at

Hitherto unknown aerial courtship displays of Black Storks *Ciconia nigra* recorded for the most part during population surveys in northern and eastern Austria between 1979-1991 are described. Aerial displays were seen mainly during early stages of the breeding cycle in April till mid-May (Fig. 1). They are characterized by mates soaring tight together in a highly synchronized manner above the nest-site or in other parts of the home range (Parallel Soaring). Additionally, melodious flight calls are given by both partners and the white undertail-coverts are widely spread. Occasionally soaring birds were seen whiffing or performing simultaneous darting flights (Fig. 3). According to (1) the regular participation of both breeding partners, (2) their regular performance around nest sites and/or within home ranges, (3) their largely restricted occurrence during early stages of the breeding cycle as well as (4) by their specific pattern of stereotyped and elaborated behavioural elements (Parallel Soaring, Displaying the Undertail-Coverts, Flight Calls, Whiffing and Darting Flights) ceremonial flights in Black Storks may generally operate as highly ritualised courtship flights. Thus, analogous to aerial displays in other large forest-living birds – like in many raptors – they may help in pointing out nest-sites to potential mates, stimulate pair formation and assist in spacing by discouraging other birds from settling close. The highly elaborated courtship flights in Black Storks seem to be unique within the “typical” storks of the tribe Ciconiini and coincide with the solitary nesting habit of the species within the closed canopies of heavily wooded areas.

Key words: behaviour, Black Stork, *Ciconia nigra*, thermal soaring, aerial displays, courtship flight, pair formation, spacing

Ključne besede: vedenje, črna štoklja, *Ciconia nigra*, dviganje na termičnem vzgorniku, dvorjenje v zraku, snubitveni let, oblikovanje para, razporejanje

1. Introduction

Pair formation and courtship behaviour among storks Ciconiidae is quite uniform, consisting of highly stereotyped behavioural patterns that have evolved as social signals through the process of ritualization. Most of the social displays of colonial and semi-colonial nesting “typical” storks of the tribe Ciconiini more closely studied by KAHL (1972A) work as short range signals at the nest-site or its immediate vicinity, whereas most species appear to ignore each other

away from the nest in the feeding areas (KAHL 1971, 1972B, KING 1988, HANCOCK *et al.* 1992). As KUSHLAN (1977) has demonstrated by field experiments in the freshwater marshes of the Everglades in southern Florida, highly visible white plumage colorations in ciconiiform wading birds act as long-distance stimuli for the formation and local enhancement of feeding aggregations. In the same way in storks with white, maximally visible plumages nesting in open habitats, like the palearctic White Stork *Ciconia ciconia*, just standing around conspicuously at the nest may oper-

ate as a long-distance signal for conspecifics announcing occupation of the nest-site and/or breeding colony (SCHÜZ 1944).

Nest-sites of Black Storks *Ciconia nigra* are normally hidden within the canopy of closed woodlands. The behaviour patterns and social displays of the solitary nesting species, which is distributed throughout the closed and more open woodlands of the warmer boreal and warm temperate climatic zones of Europe and northern Asia with smaller and more isolated populations on the Iberian Peninsula and in southern Africa, are described in more detail by SIEWERT (1932) and KAHL (1972A). Their investigations done almost exclusively by observing from hides at occupied nest-sites failed to confirm the existence and social significance of display flights during pair formation hitherto noticed just incidentally in ROHWEDER (1905), BAUER & GLUTZ VON BLOTZHEIM (1966) as well as SCHRÖDER & BURMEISTER (1974). In this paper field observations of aerial courtship displays for the most part published by SACKL (1993) and their significance for pair formation and courtship behaviour in Black Storks will be investigated.

2. Methods and materials

Between 1979 and 1991, aerial displays were observed incidentally on 18 occasions during nesting and population surveys of Black Storks in northern and southeastern Austria. On the average, breeding density of Black Storks in their continuous Austrian breeding area is about 0.4 breeding pairs (bp)/100 km² reaching up to 0.8 and 2.9 bp/100 km² in the main study areas in the Waldviertel (Lower Austria) and the prealpine lowlands of southeastern Styria, respectively (SACKL 1985, unpubl. data). In a 380 km² heavily wooded study area in the district of Fürstenfeld in eastern Styria nearest neighbour distances of simultaneously occupied nest-sites (cf. CLARK & EVANS 1954) vary from 1.3–11.1 km (\bar{x} = 3.6 km, s = 2.8, n = 11). To collect data on nest occupation and breeding success, 6–13 nests and the home ranges of additional 5–15 breeding pairs were visited annually at least twice during the breeding season from the end of March till August. Additional surveys were done occasionally by observing the birds from elevated landmarks within the home ranges of selected breeding pairs during the courtship and laying period from late March till early May. In 1979–1982, three pairs were investigated more closely by visiting nest-sites on a weekly routine. So far as possible under field conditions birds were aged and sexed according to BAUER & GLUTZ VON BLOTZHEIM (1966) and CRAMP

(1977). For this paper, materials of the author were complemented by occasional observations of aerial displays made by FRANZ SAMWALD and OTTO SAMWALD in southeastern Austria (n = 5) as well as by personal reports from M. FORSBERG, J. PRIEDNIEKS and M. STRAZDS (n = 3) recorded in Latvia between 1990–1993.

3. Results and discussion

3.1. Seasonal occurrence and social context

With a frequency of 63.7% of all locomotion flights observed in Austria 1979–1991 (n = 171) thermal soaring of one or both partners, relying on thermal upcurrents of air gaining altitude and then gliding for 3 to >6 kilometres, slowly losing height, is like in other ciconiiforms the most frequent method of locomotion of nesting Black Storks between nest and feeding sites. In early stages of the breeding cycle from April to May and again in August, after the young have fledged, single birds as well as groups of two to up to 8 individuals were seen more frequently soaring in heights estimated from 200 – approx. 1.500 metres above nest-sites and home ranges than during the feeding period in June and July (cf. Fig. 1).

Although during the hot months of summer from late June to mid-August nesting Black Storks were seen using thermal soaring for early morning as well as late afternoon feeding trips, according to its dependence from the formation of upcurrents of warm air during late morning, thermal soaring is used most frequently for the locomotion between nest and feeding sites around midday from 10 a.m. to 4 p.m. (Fig. 2).

Ceremonial flights, characterized by elaborated and highly stereotyped behavioural patterns described below, were performed on three occasions (11.5%) by single birds and in 23 or 88.5% of all 26 observation bouts available by two birds according to sex and high synchronization of behaviour regarded as breeding partners. 84.6% of all ceremonial flights of single birds as well as mates were performed shortly after their arrival at the nest-site in spring (first observations at the nest-site 15.3.–2.4., median date = 28.3., n = 10, SE Austria 1980–1990) between early April and mid-May (Fig. 1). On three occasions aerial displays were seen in June, July, and in early August, respectively. According to the participation of birds with immature plumages initially paired birds or those who had bred unsuccessfully were involved in two of these cases (M. STRAZDS, in lit.). Once a pair was also encountered performing ceremonial flights

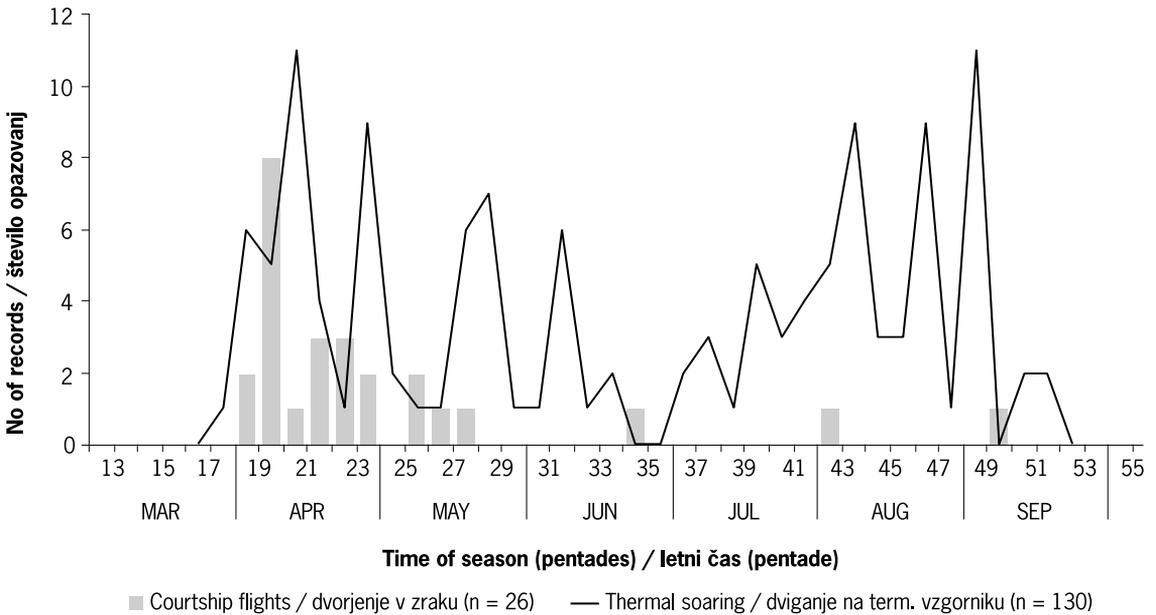


Figure 1: Seasonal occurrence of thermal soaring and courtship flights in Black Storks *Ciconia nigra* in northern and eastern Austria between 1979-1991 (three occasional records of courtship flights from Latvia 1990-1993 included)

Slika 1: Sezonsko termalno poletavanje visoko proti nebu in snubitveni leti črne štokrlje *Ciconia nigra* v severni in vzhodni Avstriji v letih 1979-1991 (skupaj s tremi naključnimi zapisi snubitvenih letov iz Latvije v letih 1990-1993)

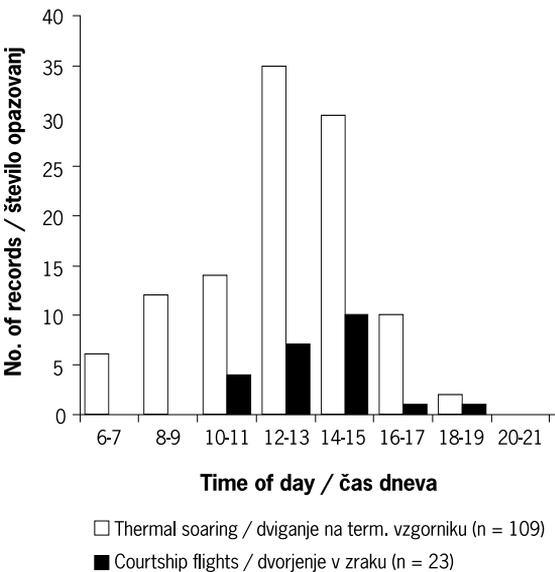


Figure 2: Diurnal frequencies (two-hour intervals) of thermal soaring and courtship flights in nesting Black Storks *Ciconia nigra* in northern and eastern Austria during 1979–1991

Slika 2: Dnevne frekvence (dveurni intervali) termalnega poletavanja proti nebu in snubitvenih letov gnezdečih črnih štokrlj *Ciconia nigra* v severni in vzhodni Avstriji v obdobju 1979-1991

within its home range in early September (cf. Fig. 1). Furthermore, 68.2% of all courtship flights by pairs for which actual nesting sites were known were performed above tree tops in the immediate vicinity of the nest-site, on all other occasions in other parts within the home range 3–5 kilometres from the nest. On at least three occasions ceremonial flights were finished by both partners disappearing close to each other in the canopy very close to the nest-site. This was followed on one occasion by an Up-down display and simultaneous preening behaviour of both partners in the nest. In another case of obviously initially paired mates landing in late April in a dry fish pond away from the nest the adult male tried for several times to copulate with its subadult mate.

3.2. Behaviour patterns of courtship flights

Courtship flights of Black Storks as illustrated in Fig. 3 are characterized by four clearly distinguishable behaviour patterns:

1. Parallel Soaring (Synchronkreisen): Soaring of both mates in a highly synchronized manner, flying tight together one after and/or closely above the other, generally 5–30 metres above tree tops – but sometimes also much higher – is the basic character

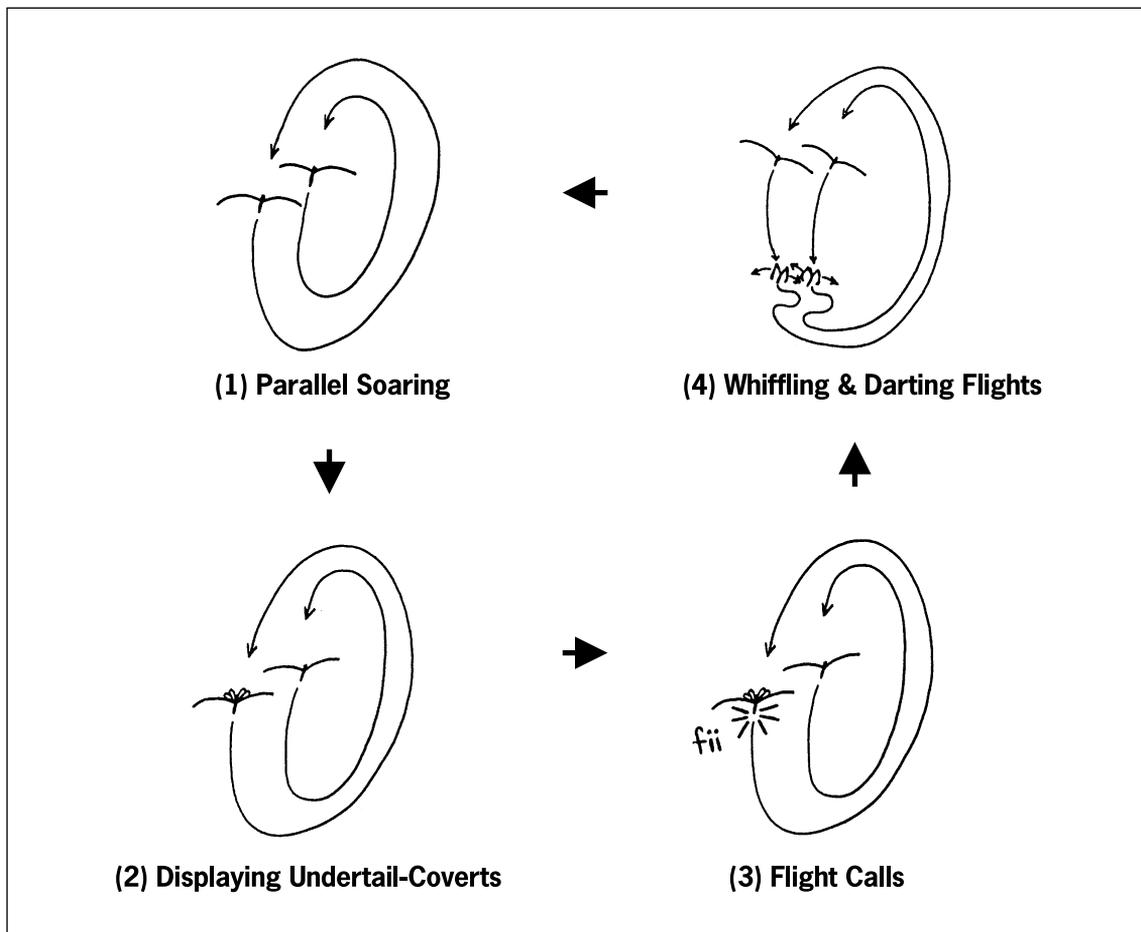


Figure 3: Schematic synopsis of the behavioural elements of courtship flights in Black Storks *Ciconia nigra*

Slika 3: Shematični pregled vedenjskih elementov snubitvenih letov črne štoklje *Ciconia nigra*: (1) vzporedno dviganje, (2) razkazovanje podrepnih krovcev, (3) oglašanje v zraku in (4) sunkovito pihanje in pikiranje

of all courtship flights. Although Parallel Soaring was performed at times 3–5 kilometres from the nest, birds were usually seen circling in this manner 5–20 minutes in an area <500 metres around the nest-site. According to its dependence on thermal upcurrents of air for Parallel Soaring courtship flights were, like thermal soaring, performed generally between early morning and late afternoon feeding bouts from the late morning hours onwards to mid-afternoon (Fig. 2).

2. Displaying the Undertail-Coverts (Flaggen): In the course of 53.9% of all courtship flights observed by one of the birds involved the white undertail coverts were widely spread protruding conspicuously out the laterally compressed black tail feathers (Fig. 4). On all occasions, when position and/or sex were noticed (for both categories $n = 5$), only the leading

bird and/or the male was seen spreading its undertail-coverts. Displaying the undertail-coverts is also a component of the Head-Shaking Crouch and Up-down display of *C. nigra* and other “typical” storks (KAHL 1972A). There is a strong resemblance of this behaviour to the displaying of the white undertail-coverts during aerial displays in some raptors like the highly syntopic Goshawk *Accipiter gentilis* and Sparrowhawks *A. nisus*.

3. Flight Calls (Flugrufe): Sometimes birds were heard to utter soft, melodious “fi”-, “diuu”- or “hi”-calls differing from calls given during Up-down and threat displays at the nest. These calls seem to be equivalent to the rarely heard flight calls mentioned in BAUER & GLUTZ VON BLOTZHEIM (1966). At least on one occasion calls were given beyond any doubt by

both birds lifting up their heads and necks during soaring as well as simultaneously lowering both legs when calling. In some other cases soaring birds bend down their necks and shake the head horizontally like in Head-shaking Crouches and Up-down displays (cf. BAUER & GLUTZ VON BLOTZHEIM 1966, KAHL 1972A, CRAMP 1977).

4. Whiffing and Darting Flights (Schaukel- und Wuchtelflüge): On rare occasions (in 5 or 19.2% of all observation bouts) soaring birds were seen whiffing simultaneously (Schaukelflug) or performing sudden simultaneous darting flights diving steeply 5–10 metres from their route and rolling during the dive from one side to the other (Wuchtelflug), resembling the better known song-flights of Lapwings *Vanellus vanellus*. Thereafter Parallel Soaring was continued. Whiffing and in particular darting flights may possibly have evolved from hostile pursuit flights occurring in many storks during initial stages of pair formation and occupation of nest-sites.

4. Conclusion

Display flights of Black Storks clearly differ from other forms of locomotion flights as thermal soaring by (1) the regular participation of both breeding partners, (2) their regular performance around nesting sites and/or within the home range, (3) their largely restricted occurrence during early stages of the breeding cycle in April and May as well as (4) by their specific pattern of highly stereotyped and elaborated behavioural elements (Parallel Soaring, Displaying the Undertail-Coverts, Flight Calls, Whiffing and Darting Flights). According to these characteristics they generally may function as aerial courtship displays by pointing out nest-sites to potential mates and neighbours, stimulating pair formation and synchronization of mates.

In many solitary nesting species of storks birds return to the same nest year after year and remate with the same partner. In the case of such rematings many courtship displays are subdued or even lacking



Figure 4: Adult Black Stork *Ciconia nigra* displaying the white Undertail-Coverts while soaring close to its nest-site, April 30th 1999, Steyrtal, Upper Austria (photo: Norbert Pühringer)

Slika 4: Odrasla črna štoklja *Ciconia nigra* razkazuje svoje bele podrepne krovce med poletom visoko proti nebu v bližini svojega gnezdišča; 30.4.1999, Steyrtal, Gornja Avstrija (foto: Norbert Pühringer)

(KAHL 1972A). Without regard to general difficulties in observing Black Storks aside nest-sites in their heavily vegetated nesting habitats, this may be the reason why up to now aerial courtship displays have been overlooked by most researchers and are noticed just incidentally throughout literature. Like courtship and other social displays in many other storks, courtship flights in Black Storks are most frequent during early stages of the breeding cycle and gradually wane during the breeding and nestling period. In palearctic White Storks and other species the resur-rection of courtship behaviour like greeting displays, nest construction and copulating when young have fledged in late summer is a well known phenomenon. Accordingly, the occasional reappearance of courtship flights in Black Storks near the end of the breeding season (or after the loss of nests earlier during the breeding cycle) is not contradictory to their importance for the occupation of nest-sites and pair formation in spring (SCHÜZ 1943AB, KAHL 1978, CREUTZ 1988).

Although some other forms of aerial displays are known to exist in other storks, the highly elaborated courtship flights of Black Storks seem to be unique within the "typical" storks of the tribe Ciconiini and coincide with the solitary nesting habits of the species in heavily wooded areas, differing from other colonial and semi-colonial storks nesting in more open wetland and savannah habitats (KAHL 1971, 1972AB). Flying in the energetically most economical form by using thermal upcurrents of air for soaring high above nest-sites (cf. RÜPPELL 1975, ALEXANDER 1982), which are normally hidden within the canopy of their forest nesting habitats, and performing conspicuous darting flights as well as displaying simultaneously maximally visible optical signals like their white undertail-coverts are important components of the courtship behaviour of many large forest-living birds. In particular many solitary nesting raptors point out nest-sites in this way to potential mates as well as to neighbours and intruders (NEWTON 1979). Thus, analogous to the aerial displays of raptors courtship flights of Black Stork, may also assist in spacing by discouraging other birds from settling close. In the same way BUXTON *et al.* (1978) explained the regular soaring of both sexes above nest-sites in solitary nesting Shoebills or Whale-headed Storks *Balaeniceps rex* as a form of territorial advertisement. For practical use during population surveys, systematically collected recordings from elevated landmarks and the mapping of courtship flights in spring from early April till mid-May may produce valuable information on the location of nest-sites, home ranges and breeding densities (SCHNEIDER-JACOBY 1999).

Evolutionarily courtship flights of Black Storks may be derived from locomotion flights as thermal soaring or hostile pursuit flights occurring during initial stages of nest occupation and pair formation. Courtship flights of Black Storks very probably are homologous to some other forms of more slightly ritualised and little known aerial displays in other storks, like the Flying Around display observed by KAHL (1972C) in all living species of wood-storks of the genus *Mycteria*. In White Storks similar flights around the nest-site following the intrusion of opponents ("Demonstrationsflug") were described recently by LAKEBERG (1993). According to KAHL (1972A), the unique Mock Fighting displays in Abdim's Stork *Ciconia abdimii* sometimes end by performing erratic bat-like darting flights. However, the only other "typical" stork in which elaborated aerial courtship displays may exist is the little studied, solitary nesting Woolly-necked Stork *C. episcopus* of the tropical wetlands and open woodlands of Africa and southern Asia (MACKWORTH-PRAED & GRANT 1973, BROWN *et al.* 1982, HANCOCK *et al.* 1992). So far as the evolution of highly ritualized courtship flights in storks really coincides with their solitary nesting habits within the canopy of heavily vegetated areas, the existence of similar behaviour patterns in other forest-living storks may be expected, like in the recently discovered and little known Storm's Stork *C. stormi* of peninsular tropical Asia (cf. HANCOCK *et al.* 1992, DANIELSEN *et al.* 1997).

5. Povzetek

Avtor obravnava do danes neznano obliko dvorjenja črnih štokelj *Ciconia ciconia* v zraku, večinoma zabeleženo med popisovanjem ptičjih populacij v severni in vzhodni Avstriji med letoma 1979 in 1991. Dvorjenja v zraku so bila opazovana predvsem v zgodnjih fazah gnezditvenega obdobja, in sicer od aprila do sredine maja (sl. 1). Glavna značilnost dvorjenja črne štoklje je naglo in nadvse sinhrono dviganje para proti nebu skupaj nad gnezdiščem ali drugod v njunem domačem okolišu (vzporedno dviganje). Oba partnerja hkrati spuščata melodične glasove in razgaljata podrepne krovce. Tu in tam so proti nebu dvigajoči se pari sunkovito pihali ali pa so simultano pikirali proti tlam (sl. 3). Glede na (1) redno sodelovanje obeh gnezdečih partnerjev, (2) njihovo stalno nastopanje nad gnezdiščem in/ali domačim okolišem, (3) njihovo v veliki meri zmanjšano pojavljanje v zgodnjih fazah njihovega gnezditvenega obdobja in (4) tudi glede na značilni vzorec njihovih stereotipnih in dovršenih vedenjskih vzorcev (vzporedno dviganje, razkazovanje podrepnih

krovcev, oglašanje v zraku, sunkovito pihanje in pikiranje) se zdi, da so obredni poleti črnih štokelj visoko ritualizirani snubitveni leti. Analogno z razkazovanjem drugih velikih gozdnih ptic v zraku – na primer mnogih plenilcev – morebiti pomagajo pri sporočanju morebitnim partnerjem, da je tu gnezdišče, stimulirajo oblikovanje parov in pomagajo pri razporejanju parov z odganjanjem tekmecev. Izredno dovršeni snubitveni leti črnih štokelj se zdijo enkratni med "tipičnimi" štokljami iz plemena Ciconiini in so povsem v skladu s solitarnimi gnezditvenimi navadami te ptičje vrste znotraj s krošnjami zaprtih in gostih gozdnatih območij.

6. References

- ALEXANDER, R.M. (1982): Locomotion of Animals. Tertiary Level Biology, Blackie, Glasgow and London.
- BAUER, K.M. & U.N. GLUTZ VON BLOTZHEIM (1966): Handbuch der Vögel Mitteleuropas, Bd. 1. Akad. Verlagsges., Wiesbaden.
- BROWN, L.H., E.K. URBAN & K. NEWMAN (1982): The Birds of Africa, Vol. 1. Academic Press, London.
- BUXTON, L., J. SCLATER & L.H. BROWN (1978): The breeding behaviour of the Shoebill or Whale-headed Stork *Balaeniceps rex* in the Bangweulu Swamps, Zambia. E. Afr. Wildl. J. 16: 201-220.
- CLARK, P.J. & F.C. EVANS (1954): Distance to nearest neighbour as a measure of spatial relationships in populations. Ecology 35: 445-453.
- CRAMP, S. (1977): Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic, Vol. 1. Oxford University Press, Oxford.
- CREUTZ, G. (1988): Der Weißstorch. Neue Brehm-Bücherei 375, 2. Aufl., A. Ziemsen, Wittenberg Lutherstadt.
- DANIELSEN, F., R. KADARISMAN, H. SKOV, U. SUWARMA & W.J.M. VERHEUGT (1997): The Storm's Stork *Ciconia stormi* in Indonesia: breeding biology, population and conservation. Ibis 139: 67-75.
- HANCOCK, J. A., J. A. KUSHLAN & M. P. KAHL (1992): Storks, Ibises and Spoonbills of the World. Academic Press, London.
- KAHL, M.P. (1971): Social behavior and taxonomic relationships of the storks. Living Bird 10: 151-170.
- KAHL, M.P. (1972A): Comparative ethology of the Ciconiidae. Part 4. The "typical" storks (genera *Ciconia*, *Sphenorhynchus*, *Dissoura* and *Euxenura*). Z. Tierpsychol. 30: 225-252.
- KAHL, M.P. (1972B): A revision of the family Ciconiidae (Aves). J. Zool., Lond. 167: 451-461.
- KAHL, M.P. (1972C): Comparative ethology of the Ciconiidae. The wood-storks (genera *Mycteria* and *Ibis*). Ibis 114: 15-29.
- KAHL, M.P. (1978): Wonders of Storks. Dodd, Mead & Co., New York.
- KING, C.E. (1988): An ethological comparison of three storks: *Ciconia boyciana*, *C. ciconia* and *C. maguari*. M.S. Thesis, Oklahoma State Univ., Stillwater.
- KUSHLAN, J.A. (1977): The significance of plumage colour in the formation of feeding aggregations of ciconiiforms. Ibis 119: 361-364.
- LAKEBERG, H. (1993): Zur Nahrungsökologie des Weißstorchs *Ciconia ciconia* in Oberschwaben: Raum-Zeit-Nutzungsmuster und Territorialverhalten. M.S. Thesis, Univ. Tübingen.
- MACKWORTH-PRAED, C. W. & C. H. B. GRANT (1973): African Handbook of Birds. Ser. 1, Vol. 1, Birds of Eastern and Northern Africa. Longmans, Green & Co., London.
- NEWTON, I. (1979): Population Ecology of Raptors. T. & A.D. Poyser, Berkhamsted.
- ROHWEDER, J. (1905): Der schwarze Storch, *Ciconia nigra* (L.). In: C.R. HENNICKE (Ed.), Naumann, Naturgeschichte der Vögel Mitteleuropas, Bd. 6, 320-328, E. Köhler, Gera-Untermhaus.
- RÜPPELL, G. (1975): Vogelflug. Kindler, München.
- SACKL, P. (1985): Der Schwarzstorch (*Ciconia nigra*) in Österreich – Arealausweitung, Bestandsentwicklung und Verbreitung. Vogelwelt 106: 121-141.
- SACKL, P. (1993): Beobachtungen zum Thermiksegeln und zur Flugbalz des Schwarzstorchs (*Ciconia nigra*). Ökol. Vögel 15: 1-16.
- SCHNEIDER-JACOBY, M. (1999): Breeding distribution and ecology of the Black Stork *Ciconia nigra* in the Sava alluvial wetlands, Croatia. Acrocephalus 20: 167-176.
- SCHRÖDER, P. & G. BURMEISTER (1974): Der Schwarzstorch. Neue Brehm-Bücherei 468, A. Ziemsen, Wittenberg Lutherstadt.
- SCHÜZ, E. (1943A): Bewegungsnormen des Weißen Storchs. Z. Tierpsychol. 5: 1-37.
- SCHÜZ, E. (1943B): Über die Jungenaufzucht des Weißen Storchs (*C. ciconia*). Z. Morph. Ökol. Tiere 40: 181-237.
- SCHÜZ, E. (1944): Nest-Erwerb und Nest-Besitz beim Weißen Storch. Z. Tierpsychol. 6: 1-25.
- SEWERT, H. (1932): Störche. Erlebnisse mit dem Schwarzen und Weißen Storch. D. Reimer & E. Vohsen, Berlin.

Arrived / Prispelo: 26.11.1999

Accepted / Sprejeto: 12.12.2000