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The evolution of nest construction in swallows (Hirundinidae) is associated with the decrease of clutch size

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A b s t r a c t : Variability of the nest construction in swallows (Hirundinidae) is more diverse than in other families of oscine birds. I compared the nest-building behaviour with pooled data of clutch size and overall hatching success for 20 species of swallows. The clutch size was significantly higher in temperate cavity-adopting swallow species than in species using other nesting modes including species breeding in evolutionarily advanced mud nests (P<0.05) except of the burrow-excavating Bank Swallow. Decrease of the clutch size during the evolution of nest construction is not compensated by the increase of the overall hatching success.

K e y w o r d s : Hirundinidae, nest construction, clutch size, evolution

Birds use distinct methods to avoid nest-predation: active nest defence, nest camouflage and concealment or sheltered nesting. While large and powerful species prefer active nest-defence, swallows and martins usually prefer construction of sheltered nests (LLOYD 2004). The nests of swallows vary from natural cavities in trees and rocks, to self-excavated burrows to mud retorts and cups attached to vertical faces.

Much attention has been devoted to the importance of controlling for phylogeny in comparative tests (HARVEY & PAGEL 1991), including molecular phylogenetic studies of swallows (WINKLER & SHELDON 1993). Interactions between the nest-construction variability and the clutch size, however, had been ignored. The only results focusing on western Palearctic parids, published by MÖNKKÖNEN & OREL (1997) and MÖNKKÖNEN & MARTIN (2000), showed discrepancies demanding following research. I therefore focused on possible relationships between clutch size and the nest construction strategy of swallows as the evolutionary innovation appearing in this group (WINKLER & SHELDON 1993).

For each swallow species I pooled population level information about clutch sizes and breeding success if any data were available, and compared it with the construction mode (Table 1). Nest construction behavior can vary among populations, but only populations with the same mode of nest construction were taken. Data presented were divided into two groups (Table 1) – the first for swallows breeding in temperate areas and the second one for swallows occuring in tropical and Southern Hemisphere regions. Tropical zone and Southern Hemisphere species of swallows generally lay smaller clutches than their close relatives in temperate regions as known in other birds (MARTIN et al. 2000, GHALAMBOR & MARTIN 2001). This part of clutch size variation may be explained by Ashmole`s hypothesis (ASHMOLE 1963, RICKLEFS 1980, GRIEBELER & BOHNING-GAESE

2004) about the seasonality of resources in temperate regions. In tropical regions, swallows generally tend to the sheltered nesting. ALERSTAM & HÖGSTEDT (1981) had speculated that this tendention is probably more profound in the tropics, where is a great proportion of predators, mainly snakes and mammals (cf. ROYAMA 1969 and EARLÉ 1981). Increased predation risk seems to raise the common strong correlation between exposed foraging (typical for all swallows) and sheltered nesting.

There are five modes of nest construction – mud nest retoir builders (*Petrochelidon*, *Cecropis*), covered mud cup builders (*Delichon*), open mud cup builders (*Hirundo* and *Ptyonoprogne*), burrow excavators (*Riparia*, *Pseudohirundo*) and species adopting the previously excavated burrow (New World members of the martin clade like *Progne*, *Stelgidopteryx* or *Tachycineta*) (WINKLER & SHELDON 1993). There is no indication that any of construction modes arose more than once during the evolution of swallow species (MAYR & BOND 1943). All species except the last named group spent approximately an identical amount of time building the nest; e. g. 8-18 days in House Martins (LIND 1960); excavating of a burrow by Bank Swallows takes about 1-16 days (ASBIRK 1976) – the burrow is shorter in worse material (HENEBERG 2003). This fact raises an objection to the influence of energy costs of the burrow excavation, which may misrepresent the only one results published on parids (MÖNKKÖNEN & MARTIN 2000).

The clutch size is highest in the group of temperate species adopting previously excavated cavities (5.24 eggs). Differences between the pooled clutch size of temperate adopters and species using other modes of nest construction were significant in all cases (all one-tailed χ^2-tests $P<0.05$) except of the burrow excavators group (Bank Swallow) ($P>0.1$). Yet, a small proportion of population data for swallows breeding in the tropical and subtropical zone provide non-significant results for this group of family Hirundinidae. But there is no reason to presume any different results in swallows breeding in non-temperate regions.

There are two basic independent hypotheses for the evolution of nest construction. WINKLER & SHELDON (1993) found that ontogeny of mud-nest construction recapitulates the phylogeny of nest types from open cups through closed cups to retorts. These authors also suggest that adopters and mud-nesters arose independently from burrowing ancestors. The second hypothesis presented by SIBLEY & AHLQUIST (1982) is based on the single copy DNA-DNA hybridization as well as the first one. Their results indicate that adoption of cavities as found in Rough-winged Swallows or Purple Martins is the primitive state and other nest-building behaviour types are derived from this mode. Both these hypotheses present the building of mud nests as a key innovation allowing mud nesters to occupy habitats lacking available nest cavities or substrates for burrowing (WINKLER & SHELDON 1993). The ability to lay clutches in sheltered nests causes usually the decrease of clutch size compensated by the increase of the overall hatching success (ALERSTAM & HÖGSTEDT 1981). The evolutionary innovation of mud-nesting found in some species of swallows is also associated with the decrease of clutch size, but this is not compensated by any increase of the hatching success (cf. Table 1).

Zusammenfassung

Die Evolution des Nestbaues bei Schwalben (Hirundinidae) ist mit einer Verringerung der Gelegegröße verbunden. Die Variabilität des Nestbaues ist bei Schwalben (Hirundinidae) höher als in anderen Singvogelfamilien (Oscines). Ich verglich das Nestbauverhalten von 20 Schwalbenarten anhand gepoolter Daten von Gelegegröße und Gesamtbruterfolg. Die Gelegegröße war bei Schwalbenarten aus gemäßigten Breiten, die Höhlen annehmen, signifikant höher als bei Arten mit anderen Nestern, einschließlich Arten mit evolutionär fortgeschrittenen Lehmnestern ($P < 0,05$). Eine Ausnahme ist die höhlengrabende Uferschwalbe. Die Abnahme der Gelegegröße während der Evolution des Nestbaues wird durch den Gesamtbruterfolg nicht kompensiert.

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Tab. 1. Clutch size and overall hatching success for the family *Hirundinidae*. Clutch size data are pooled according to the population value of each sample, overall hatching success is pooled according to the number of population values available. Data from the Northern Hemisphere are given in upper part of the table, data from tropical regions and Southern Hemisphere are given in lower part of this table. Data were compiled from MYRES (1957) and HAMILTON & MARTIN (1985) for the Cliff Swallow, BALÁT (1974), BRYANT (1975), KONDĚLKA (1978), BRYANT & WESTERTERP (1983) and PIKULA & BEKLOVÁ (1987) for the House Martin, KUŹNIAK (1967), PIKULA & BEKLOVÁ (1987) and GÓRSKA et al. (1999) for the European Swallow, PETERSEN (1955), ASBIRK (1976), MORGAN (1979), SIEBER (1980) and PIKULA & BEKLOVÁ (1987) for the Bank Swallow, ALLEN & NICE (1952) and HILL (1999) for the Purple Martin, LUNK in RICKLEFS (1972) for the Rough-winged Swallow, ZACH (1982), HUSSELL & QUINNEY (1986), WHEELWRIGHT et al. (1991) and MURPHY et al. (2000) (all for the Tree Swallow). Data for *Hirundo albigularis*, *H. daurica*, *H. dimidata*, *H. fuligula* and *Riparia paludicola* were compiled from MARTIN et al. (2001). SCHMIDT (1962) for the Larger Striped Swallow, EARLÉ (1989) for the Redbreasted Swallow, EARLÉ (1986) for the South African Cliff Swallow, MØLLER et al.. (2001) for the Banded Martin, TARBURTON (1991) and MAGRATH (1999) (both for Fairy Martin), DYRCZ (1981) for the Grey-breasted Martin and for the Mangrove Swallow and ALLEN (1996) for the Bahama Swallow.

Nest construction mode	Species	Clutch size	Overall hatching success (%)
adopted cavity	Rough-winged Swallow (*Stelgidopteryx ruficollis*)	6.3	61.0
adopted cavity	Tree Swallow (*Tachycineta bicolor*)	5.7	94.3
adopted cavity	Purple Martin (*Progne subis*)	4.8	62.6
burrow	Bank Swallow (*Bank Swallow*)	4.8	69.0
mud retort	Red-rumped Swallow (*Hirundo daurica*)	4.5	-
mud retort	Cliff Swallow (*Petrochelidon pyrrhonota*)	4.2	53.2
covered mud	Cup House Martin (*Delichon urbica*)	3.9	72.5
open mud cup	European Swallow (*Hirundo rustica*)	4.4	88.6
adopted cavity	Mangrove Swallow (*Tachycineta albilinea*)	4.0	62.
adopted cavity	Fairy Martin (*Hirundo ariel*)	3.5	70.7
adopted cavity	Grey-breasted Martin (*Progne chalybea*)	3.3	94.
adopted cavity	Bahama Swallow (*Tachycineta cyaneoviridis*)	3.0	70.0
burrow	Banded Martin (*Riparia cincta*)	3.2	-
burrow	Plain Martin (*Riparia paludicola*)	2.9	-
mud retort	Redbreasted Swallow (*Hirundo semirufa*)	3.4	60.6
mud retort	Larger Striped Swallow (*Cecropis cucullata*)	3.1	-
mud retort	South Afr. Cliff Swallow (*Petrochelidon spilodera*)	2.4	56.5
open mud cup	White-throated Swallow (*Hirundo albigularis*)	2.8	-
open mud cup	Rock Martin (*Hirundo fuligula*)	2.8	-
open mud cup	Pearl-breasted Swallow (*Hirundo dimidiata*)	2.4	-