General Introduction

1 Nests and nest-building in birds

Morphological and behavioural differences between the sexes in animals are often a result of sexual selection (Andersson 1984). In birds, conspicuous behaviours and traits like song and plumage colouration are well known to influence reproductive success through sexual selection, but the importance of nests and nest-building behaviour for reproductive success and as possible cues for mate choice received only little attention. The vast majority of birds build some sort of nest or at least choose a nest site to improve reproductive success. Nests and their location can function as protection against sun, rain, wind, heat, cold and predators (Hansell 2000). Usually the exclusive function of nests is to protect offspring. In most bird species, even if sexes differ in some other behavioural or morphological traits, both sexes together engage in nest-building, incubation and feeding of nestlings. Although a nest and raising offspring is crucial for offspring survival, it is difficult to determine the contribution of each sex to offspring survival with regard to nest-building, incubation and feeding of nestlings, if both sexes together engage in these activities. In many weaverbirds, males build nest frames without the participation of females (Skead 1956, Emlen 1957). These nest frames get accepted by females who line them and pad the inside with soft material. In these species, the contribution to offspring survival is clearly divided between the sexes: males alone build nest frames in their territory, whereas females incubate eggs and feed nestlings. In polygynous weaverbird species with the described division of labour between the sexes, male reproductive success might not only be determined by plumage characteristics or courtship behaviour, but also by the ability to build many and/or high-quality nests (Collias & Victoria 1978). Nests can influence male reproductive success in two ways. First, males with more nests built during a season can attract more females (Friedl & Klump 1999), second, females could choose males based on their nests and evaluate the quality of nests.

2 Objectives of this thesis

This PhD thesis was initiated by results of a previous study conducted by T. W. P. Friedl, who investigated various aspects of the breeding system of Red Bishops

(*Eulectes orix*; Friedl & Klump 1999, 2000, Friedl 2002, 2004). Red Bishops are a polygynous, colonially breeding weaverbird species widespread in sub-Saharan Africa. Males built nest frames which get accepted by females, whereas females incubate eggs and raise offspring without male assistance (Skead 1956), as is typical for polygynous weaverbird species, (Emlen 1957). Amongst other results, Friedl (1999) found that male reproductive success is mainly determined by the total number of nests build within a breeding season, which in turn depends on the duration of territory tenure and the number of nests built per week. The objective of the thesis presented here was to investigate various aspects of male nest-building behaviour and their influence on male reproductive success in more detail.

The first chapter analyses the influence of several aspects of nest-building ability and effort, nest characteristics, and male age on nest-building performance and reproductive success. A number of nest characteristics are tested for their influence on nest durability and matching acceptance probability. Changes in reproductive success, nest-building ability and effort with male age are investigated and discussed in light of different hypotheses (Forslund & Pärt 1995) explaining age-dependent reproductive success. In particular, the following questions are addressed in the first chapter: (1) How does male breeding performance depend on nest-building skills and effort? (2) Do females show a preference for certain nest characteristics, and if yes, do these nest characteristics influence nest durability or breeding success? (3) Do males of different age classes differ with respect to reproductive success, and if yes, are the observed differences due to reproductive effort, nest-building skills or the quality of nests built?

The second chapter deals with male time-budget allocations and nest-building efficiency in relation to nest-building performance and reproductive success. Additionally, a relation between selected behavioural patterns, especially male-male interactions, and territory tenure is tested for. Further on, a possible trade-off in the time budgets allocated to different behaviours is investigated. The following questions are addressed: (1) Do males that construct more nests during the breeding season spend more time with nest-building, and if so, are there any trade-offs with other behavioural patterns? (2) Do males that construct more nests during the breeding season build more efficiently than other males, indicating better inherent or acquired nest-building ability? (3) Independent of the number of nests built by a male, do other aspects of nest-building behaviour influence male reproductive success? (4)

In addition, I investigate whether other behavioural patterns such as the proportion of time spent with male-male interactions or courtship behaviour are related to male reproductive effort (number of nests built) or reproductive success (number of nests accepted).

The third chapter describes the Red Bishops' breeding system as a biological market with nests as a traded commodity following the considerations on biological markets by Noë & Hammerstein (1994, 1995). Temporal changes in demand for and supply of nests within a breeding season on a weekly time scale are described and their consequences for male nest-building behaviour are analysed. The timing and synchrony of male and female breeding activity and their interaction with each other and rainfall are described. Short-term adjustments in the supply of nests by males in response to increasing female demand for nests are investigated, together with an effect of such adjustments on male mating success.

The fourth chapter analyses forebrain activity in relation to nest-building behaviour. According to Jarvis & Mello (2000) it can be expected, that nuclei from all major forebrain subdivisions are involved in processing sensory and motor information of any complex behavioural pattern. Nest-building behaviour in weaverbirds is a complex sequential motor pattern and needs to be learned in the first two years of life (Collias & Collias 1964, 1973), similar to singing in passerines. It is assumed that neural control of nest-building is as complex as neural control of singing, also involving several different regions in the forebrain. Since this is the first study investigating forebrain activity in relation to nest-building behaviour in weaverbirds, all major forebrain subdivisions shall be analysed for changes in activity after nest-building. Forebrain activity is measured as protein expression of an Immediate Early Gene (IEG), ZENK. The investigation of brain area activity by the expression of IEGs is an established technique (Chaudhuri 1997). It can be applied in a variety of contexts (Long & Salbaum 1998), because the expression of IEGs is generally associated with contexts in some way important for the organism (Clayton 2000), e.g. novel contexts and memory formation. Regions involved in the control of nest-building behaviour are identified by changes in ZENK expression after nest-building. Additionally, differences between hemispheres in ZENK expression in relation to nest-building behaviour are investigated.

I hope that this thesis raises more interest in the importance of nests and nest-building behaviour, features that can determine reproductive success in addition to

other behavioural and morphological traits. Furthermore, I suggest that the investigation of neural mechanisms underlying nest-building behaviour could lead to a better understanding of the functional organisation of the avian forebrain.

3 References

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