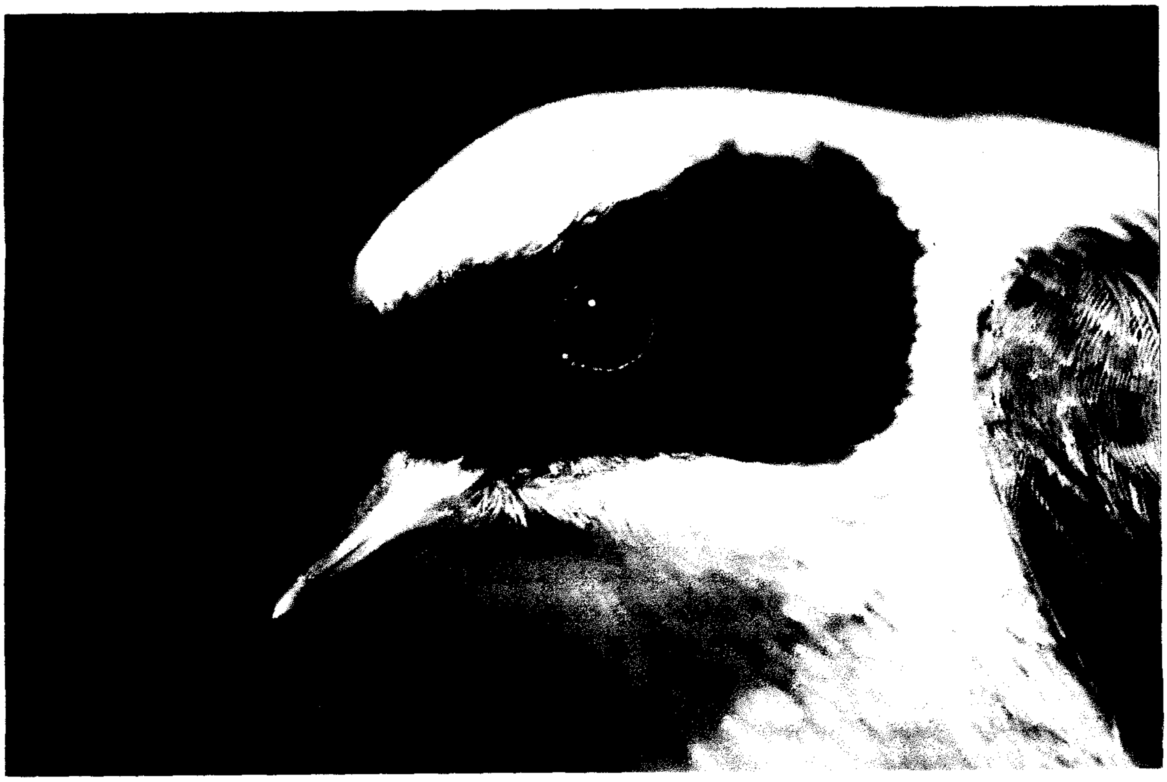
FORTPFLANZUNGSSTRATEGIEN DER BEUTELMEISE

(*Remiz pendulinus*)



Diplomarbeit

ausgeführt von Brigitte Schleicher

am Konrad Lorenz-Institut für Vergleichende Verhaltensforschung

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INHALTSVERZEICHNIS

EINLEITUNG

Fortpflanzung ist einer der beiden großen Funktionskreise biologischer Systeme. Welches Fortpflanzungssystem sich in einer Art ausbildet wird von verschiedenen ökologischen Randbedingungen, wie Lebensraum und dessen Ressourcen, bestimmt (EMLEN & ORING 1977), aber auch von den unterschiedlichen Fortpflanzungsinteressen der Geschlechter (TRIVERS 1972). Weibchen sollten durch ihre anfänglich hohe Investition (Eiproduktion) bei der Wahl ihrer Partner besonders auf deren Qualitäten, wie väterliche Fürsorge (TRIVERS 1972), verteidigte Ressourcen (WITTENBERGER 1976) oder genetische Qualität (HEISLER 1981), achten (TRIVERS 1972), während Männchen eher danach trachten sollten, ihren Fortpflanzungserfolg durch Attraktion mehrerer Weibchen zu erhöhen, da Samen eine eher billige Investition darstellen (WITTENBERGER 1979).

Im allgemeinen gilt bei Vögeln Monogamie als das häufigste Paarungssystem, zu dem ca. 90 % aller Passeriformes gezählt werden (Übersicht in LACK 1968, FORD 1983).

Monogamie ist dort ausgebildet, wo die Mithilfe des Männchens bei der Jungenaufzucht eine unabdingbare Voraussetzung für den Erfolg einer Brut darstellt (WITTENBERGER 1979, WITTENBERGER & TILSON 1980). Sobald aufgrund günstiger ökologischer Bedingungen (z.B. einem ausreichenden Nahrungsangebot) ein Partner von den elterlichen Verpflichtungen entbunden werden kann, wird die Entstehung von Polygamie möglich (VERNER & WILLSON 1966, 1969).

Es sind meistens die Männchen, die versuchen, durch eine Monopolisierung zusätzlicher Weibchen den eigenen reproduktiven Erfolg zu erhöhen (TRIVERS 1972). Polygynie ist daher bei Vögeln häufiger anzutreffen als Polyandrie (ORING 1982, MOCK 1983).

Im Gegensatz zu Polygynie sind in polyandrischen Paarungssystemen, wie bei einigen Watvögeln (z.B. JENNIE & COLLIER 1972), die Rollen der Partner meist vertauscht (siehe JEHL & MURRAY 1986). In diesen Systemen übernehmen die Männchen die Jungenaufzucht, die Weibchen verteidigen das Territorium und konkurrieren um die Männchen.

Vaterschaftsanalysen mit Hilfe von DNA-fingerprinting Methoden (BURKE et al. 1989) zeigen aber, daß es oft fließende Übergänge zwischen den verschiedenen Systemen gibt. Selbst in monogamen Paarungssystemen versuchen Männchen, neben Mithilfe bei der

Jungenaufzucht, über Fremdkopulationen ihren Fortpflanzungserfolg zu erhöhen (Überblick in BIRKHEAD & MØLLER 1992). Sie verfolgen somit parallel zwei Strategien ("mixed reproductive strategy", siehe FITCH & SHUGART 1984). Mit zunehmender Vaterschaftsunsicherheit werden jedoch Verhaltensstrategien, wie intensive Partnerbewachung wichtig, um Fremdkopulationen zu vermeiden, was allerdings mit einem hohen Zeit- und Energieaufwand verbunden ist (BIRKHEAD & MØLLER 1992).

Wo direkte Partnerbewachung nicht möglich ist, weil ein Partner in der fertilen Phase das Nest zu bewachen hat, während der anderere auf Nahrungssuche ist, wie zum Beispiel bei Greifvögeln oder kolonialen Seevögeln (BIRKHEAD et al. 1987), versuchen die Männchen durch Erhöhung der Kopulationsfrequenz mit dem eigenen Partner die Vaterschaftsunsicherheit zu verringern (BIRKEHEAD 1988). Eine weitere Strategie zur Sicherung der Vaterschaft ist Territorialität, die bei vielen Arten eingesetzt wird (GREIG-SMITH 1982, CATCHPOLE 1983, SEARCY & ANDERSSON 1986). So vergrößern Männchen dieser Arten während der fertilen Phase ihrer Partner das Territorium, um sie vor Fremdkopulationen besser schützen zu können (HINDE 1952, SNOW 1958, MØLLER 1990a).

Wenn es zu keiner vollständigen Eibefruchtung durch den eigenen Partner kommen kann (Mc KINNEY et al. 1984) oder, wenn es darum geht, die Überlebenswahrscheinlichkeit der Nachkommen durch eine Verbesserung der Gene zu erhöhen (WEATERHEAD & ROBERTSON 1979, 1981, HEISLER 1981), beteiligen sich auch die Weibchen an Fremdkopulationen (siehe SMITH 1988, MØLLER 1988). Um dazu den geeigneten Partner zu finden, ziehen die Weibchen verschiedene Kriterien heran, die mit der Qualität der Männchen in Verbindung stehen. Ist die Hilfe des Männchens bei der Jungenaufzucht wichtig, so ist die Bereitschaft der Männchen zur elterlichen Fürsorge das Paarungskriterium (TRIVERS 1972). Weibchen anderer Arten (WITTENBERGER 1976) richten sich nach dem Territorium und dessen Ressourcen, oder nach anderen Männchenqualitäten, wie morphologische Merkmale oder Verhaltensmerkmale. Auch gewisse Leistungen der Männchen, wie "Hochzeitsgeschenke" (NISBET 1977) oder die Lauben der Laubenvögel (BORGIA 1985a), gelten als wichtige Paarungskriterien (HILL 1990).

Im Falle der Beutelmeisen sollten die Strategien von Männchen und Weibchen im Rahmen ihres komplexen Paarungssystemes (siehe FRANZ 1991) untersucht werden.

Die Beutelmeise (*Remiz pendulinus*) hat laut FRANKE (1938) die Farben der Au eingefangen. Brust, Bauch und Schwanz sind cremefarben, der Nacken ist weiß bis grau gefärbt, der Rücken ist intensiv kastanienbraun und am Kopf zieht sich je nach Geschlecht eine mehr oder weniger breite schwarze Maske bis hinter die Augen.

Bild 1: Seitenansicht eines Beutelmeisenmännchens

Sie ist neben den Goldhähnchen (*Regulus regulus, R. ignicapillus*) und dem Zaunkönig (*Troglodytes troglodytes*) einer unserer kleinsten heimischen Singvögel.

Ihr vorzugsweise besiedeltes Gebiet sind Aulandschaften, wo sie an Pappeln und Weiden ihre Nester bauen (FRANZ et al. 1979, FLADE et al. 1986, PERSSON & ÖHRSTRÖM 1989). Dieses Habitat bietet ihnen neben Nistplätzen und Baumaterial (vorwiegend Schilf, Pappel- und Weidenwolle) vor allem ein ausreichendes Nahrungsangebot (FRANZ et al. 1979).

Auf der Suche nach solchen potentiellen Brutgebieten wandern Beutelmeisen zwischen den Bruten manchmal weit umher, manchmal sogar über 100 km (FRANZ et al. 1987) und erschließen oft recht unterschiedliche Lebensräume. Deren Besiedelung jedoch setzt eine gewisse Anpassungsfähigkeit voraus. Beutelmeisen im Untersuchungsgebiet zum Beispiel zeigen diese Fähigkeit, innerhalb einer Brutsaison die zuerst grünenden Aulandschaften (Donau-, Marchauen) und erst später im Jahr die ausgedehnten Schilfgebiete oder die Trockenstandorte des Neusiedlerseeraumes zu besiedeln (FRANZ 1988c).

Da in diesen Lebensräumen die Biomasseproduktion zu unterschiedlichen Jahreszeiten ihr Maximum erreicht, können die Beutelmeisen ihre Brutzeit von April bis August (FRANZ 1988c) ausdehnen und das im jeweiligen Gebiet konzentriert auftretende Nahrungsangebot nützen ("Schlaraffenlandeffekt", VERNER & WILLSON 1966, 1969). Dies ermöglicht die Aufzucht der Brut von nur einem Elter.

Bei der Entscheidung, welcher Altvogel die Brut betreuen soll, stehen die Geschlechter jedoch im Konflikt, was sich in zahlreichen Gelegeaufgaben widerspiegelt (FRANZ 1991). Welche ökologischen Randbedingungen diesem Konflikt zugrunde liegen und in welcher Weise sie die Entscheidung beeinflussen, ist noch weitgehend ungeklärt. Beide Geschlechter sollten jedoch versuchen, ihren eigenen reproduktiven Erfolg zu erhöhen (TRIVERS 1972). Meistens wird die Betreuung in der frühen Brutsaison von den Weibchen übernommen. Gegen Ende der Brutsaison werden die meist kleineren Gelege den Männchen zur Pflege überlassen (FRANZ 1991). Dadurch können sich auch die Weibchen mehrmals verpaaren (Polyandrie) und so den eigenen Reproduktionserfolg erhöhen. Nachdem nur ein Altvogel für die Aufzucht der Jungen notwendig ist, können die Männchen abwandern. Da für sie die Wahrscheinlichkeit, einen Partner zu bekommen, mit fortschreitender Brutzeit sinkt, investieren sie zu Beginn der Brutzeit in die Attraktion weiterer Paarungspartner (Polygynie), d.h. in den Bau eines weiteren Nestes und übernehmen erst gegen Ende der Brutsaison selbst die Brutfürsorge. Durch das Auftreten dieser beiden Möglichkeiten, Polygynie und Polyandrie, kann das Paarungssystem der Beutelmeise als polygynandrisch bezeichnet werden (siehe KREBS & DAVIES 1991).

Da nur ein geringer Anteil der Männchen eine Brut betreut, mag der Eindruck entstehen, daß Beutelmeisenmännchen nur wenig in die Nachkommenschaft investieren. Was sie aber von vielen Männchen der Passeriformes unterscheidet, ist die hohe Investition zu Beginn einer Brut.

Ihre Qualitäten zeigen sie nämlich, wenn sie mit großem Energie- und Zeitaufwand kunstvolle Beutelnester bauen, mit denen sie versuchen Weibchen anzulocken (FRANZ & THEISS 1983).

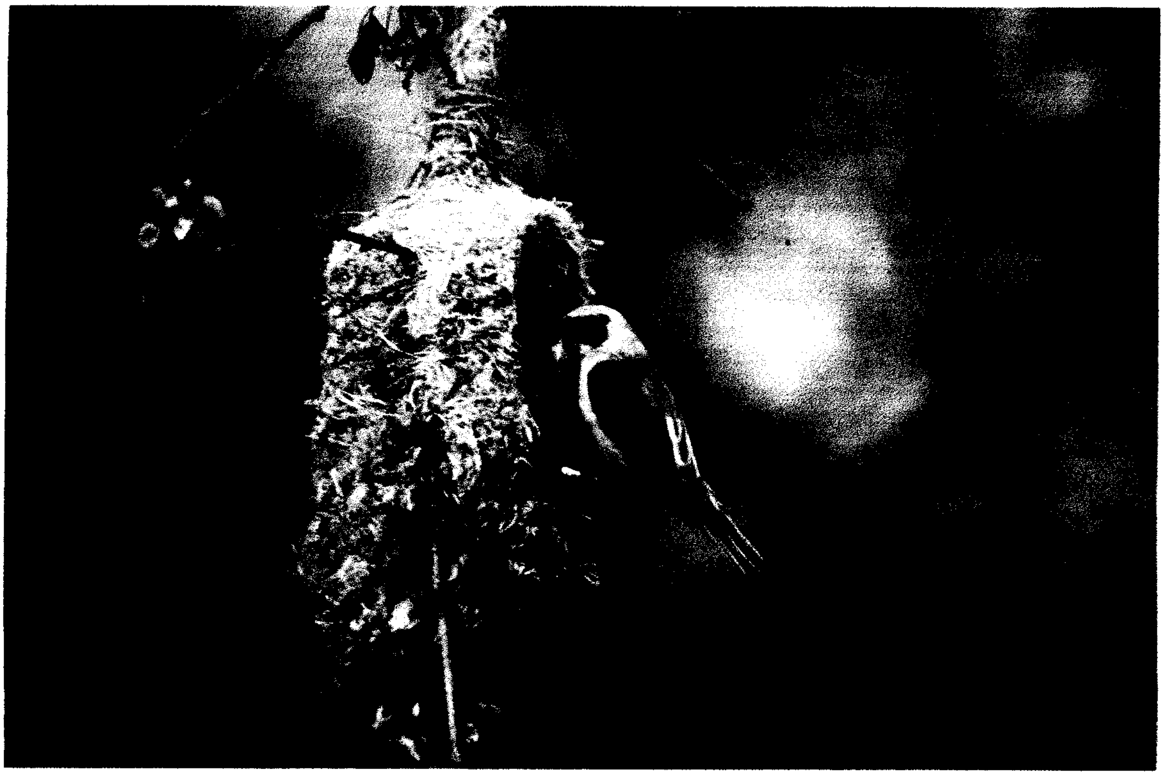


Bild 2: Beutelmeisenmännchen beim Nestbau.

Während der Bauphase können verschiedene Neststadien unterschieden werden (siehe FRANZ et al. 1979), wobei mit zunehmendem Nestbaufortschritt (Ring - Henkelkorb) der Paarungserfolg steigt. Auch bei den Webervögeln, wie zum Beispiel beim Dorfweber *Ploceus cucullatus* präsentieren die Männchen ihre kunstvoll gewebten Nester. Zusätzlich verstärken sie noch deren Anziehungskraft, indem sie mit hoher Frequenz ihre auffällige Gefiederzeichnung zur Schau stellen (COLLIAS & VICTORIA 1978). Bei vielen anderen Arten werden ebenfalls auffällige Gefiedermerkmale (MØLLER 1990) und ausgeprägte Gesänge (SEARCY & ANDERSSON 1986) zur Weibchenattraktion eingesetzt.

Da jedoch Beutelmeisen keinen ausgeprägten Geschlechtsdimorphismus oder Gesang zeigen und zudem nicht territorial sind, ist anzunehmen, daß die Nester so wie beim Dorfweber *Ploceus cucullatus* ebenfalls eine wichtige Rolle bei der Verpaarung einnehmen.

In dieser Arbeit sollen die Fortpflanzungsstrategien von Männchen und Weibchen untersucht werden, um so Einblick in diesen "Geschlechterkonflikt" zu erhalten. Im genaueren sollen einerseits die Möglichkeiten der Männchen zur Sicherung ihrer Vaterschaft untersucht werden, und andererseits soll geklärt werden, nach welchen Gesichtspunkten die Weibchen ihre Partner wählen. Die Ergebnisse sollen Aufschlüsse darüber geben, inwiefern eine gesicherte Vaterschaft und "qualitativ gute" Nester die Entscheidung "Betreuen" oder "Verlassen" einer Brut beeinflussen können.

UNTERSUCHUNGSGEBIETE UND METHODE

Untersuchungsgebiete:

Die Untersuchungen in der Brutsaison 1992 konzentrierten sich auf zwei Gebiete, die sich durch ihre geographische Lage (Abb. 1), sowie durch Klima und Vegetation unterschieden.

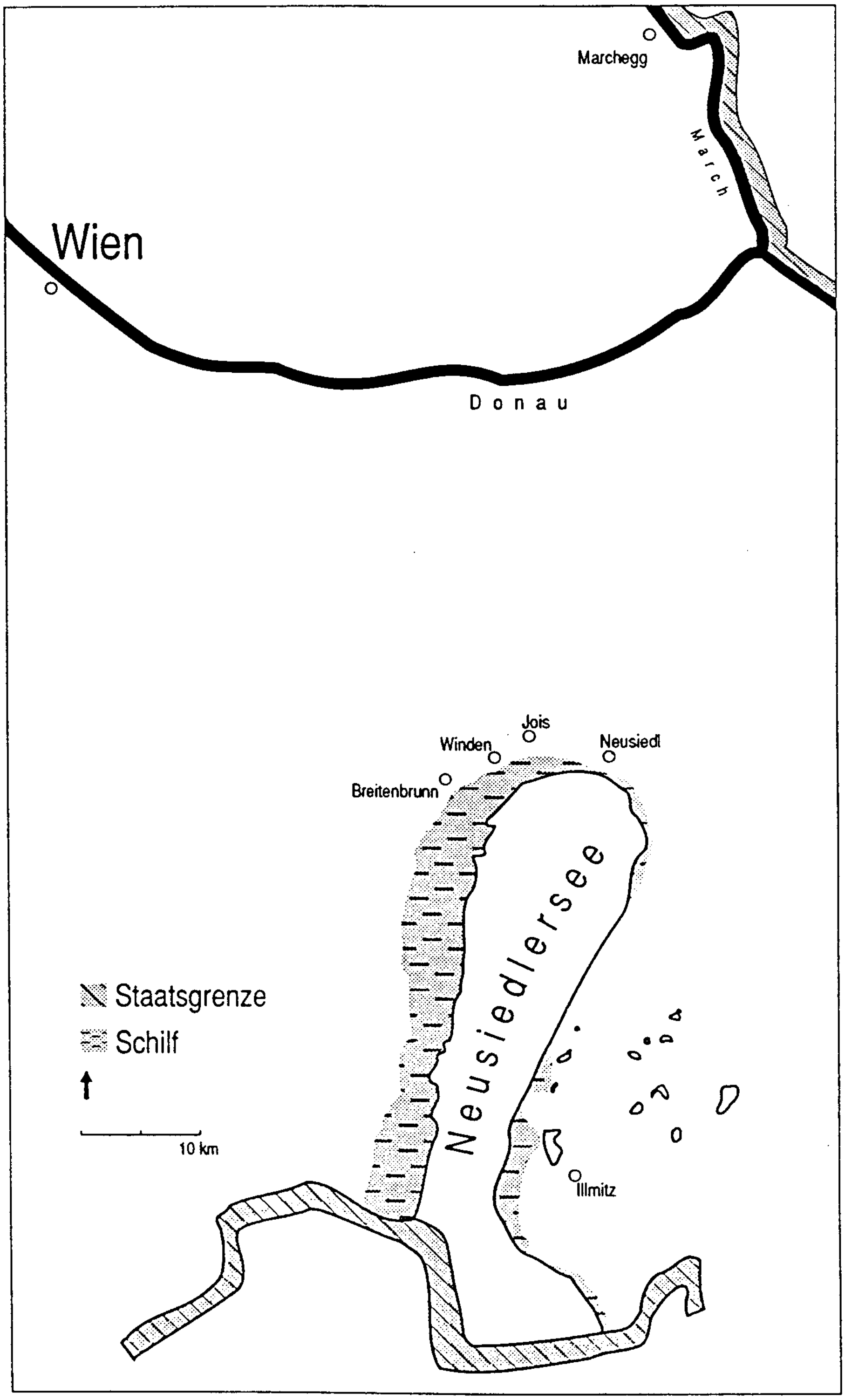


Abb. 1: Darstellung sämtlicher Untersuchungsgebiete in der Brutsaison 1992.

Die unterschiedliche Habitatzusammensetzung ist in Tab. 1 dargestellt.

Tabelle 1: **Habitatzusammensetzung** in Illmitz und Marchegg (im Umkreis von 100 m vom Nest entfernt)

	ILLMITZ n = 37	MARCHEGG n = 33
Schilf	25.3 %	13.5 %
Weiden	6.0 %	24.9 %
Pappeln	11.0 %	4.1 %
Wiesen	5.3 %	21.2 %
Hochgrasfluren	5.6 %	7.1 %
Sträucher	1.1 %	1.4 %
Wasser	2.2 %	17.4 %
Wein	12.4 %	0.0 %
Robinien	11.1 %	0.0 %
Brennessel	0.0 %	10.4 %

Die Gebiete wurden deshalb ausgewählt, da über sie schon Informationen zur Brutbiologie der Beutelmeise vorlagen (siehe dazu FRANZ 1987, 1991). So wurde in Niederösterreich (ca. 60 km von Wien entfernt) in den Marchauen bei Marchegg (48.16 N, 16.57 E) ein Auwaldstreifen entlang dem Grenzfluß March, nördlich und südlich der Marchbrücke, in der Zeit von Anfang April bis Mitte Juni 1992 täglich kontrolliert. Die Verteilung der Nester zeigt Abb. 2.

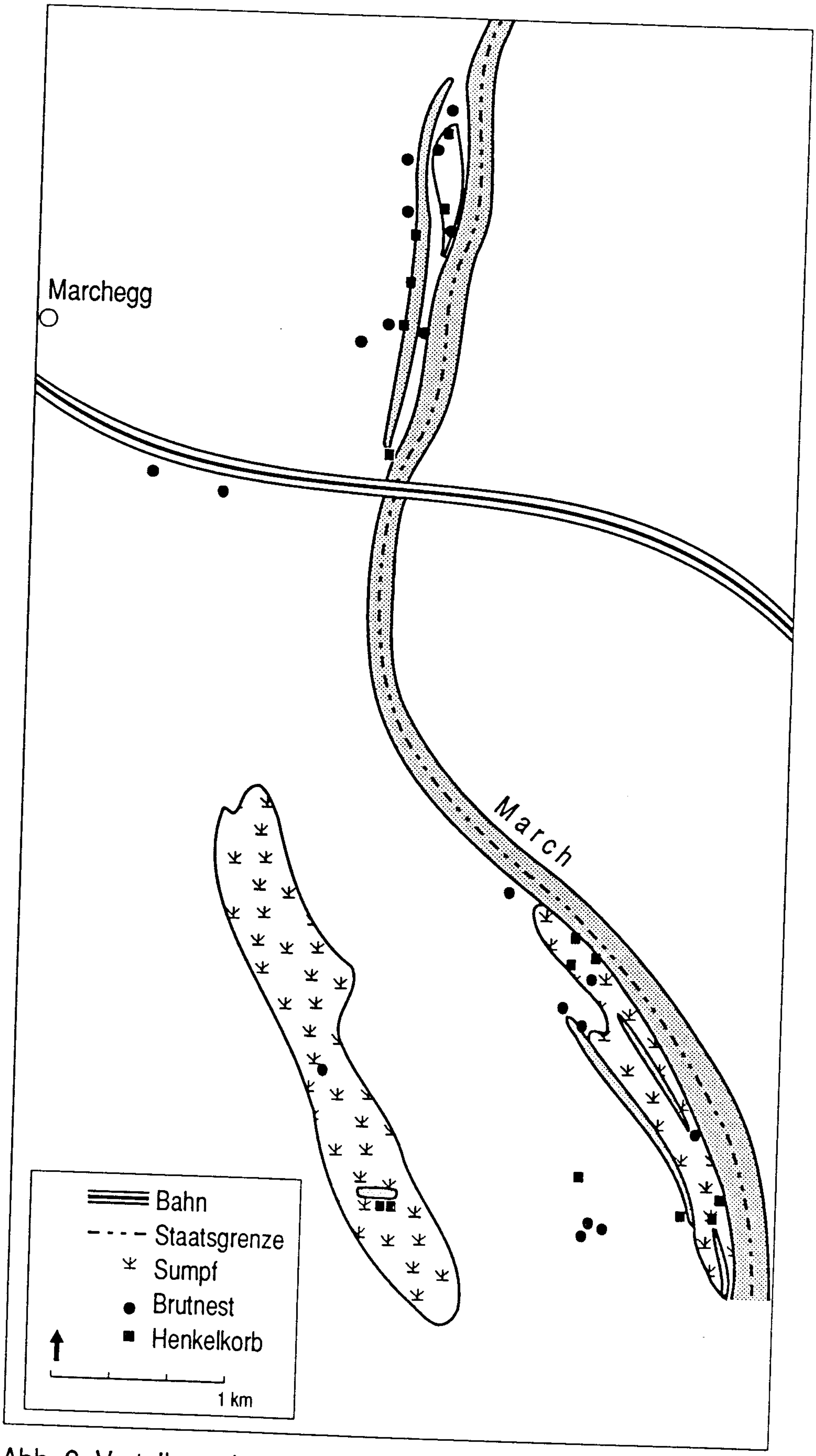


Abb. 2: Verteilung der Beutelmeisennester im Gebiet bei Marchegg von April bis Mitte Juni 1992.

In diesem Abschnitt dominieren vor allem Pappeln *Populus alba* und verschiedene Arten von Weiden, wie die Silberweide *Salix alba*, die Aschweide *S. cinerea* und die Bruchweide *S. fragilis* (Salicaceen).

Der relativ aufgelockerte Baumbestand war stellenweise von verschiedenen Straucharten, wie dem Roten Hartriegel *Cornus sanguinea* (Cornaceae), dem Gemeinen Schneeball *Viburnum opulus* (Caprifoliaceae), der Schwalbenwurz *Vincetoxicum hirundinaria* (Asclepiadaceae), der Gemeinen Waldrebe *Clematis vitalba* (Ranunculaceae), dem Schwarzen Holunder *Sambucus nigra* (Caprifoliaceae) und dem Eingriffeligen Weißdorn *Crataegus monogyna* (Rosaceae), um nur einige zu nennen, durchsetzt. Der Unterwuchs bestand häufig aus einem ausgedehnten Schilfbestand *Phragmites communis*, in flußnahen Zonen herrschten jedoch Brennessel *Urtica dioica* vor. In der Probefläche sind neben den Auwäldchen sowohl baumbestandene Altwasserarme als auch selten (nur einmal im Untersuchungszeitraum) gemähte Feuchtwiesenbereiche mit den zugehörigen typischen Pflanzenarten eingeschlossen.

Im Gegensatz dazu befindet sich die zweite Probefläche im Burgenland (ca. 60 km von Wien entfernt) sowohl am West-, als auch am Ostufer des Neusiedlersees (siehe Abb. 1).

Das Gebiet bei Illmitz im Osten des Sees (47.46 N, 16.48 E) wird durch die Eckpunkte Sandeck, Kiesgrube zwischen Illmitz und Podersdorf sowie dem Illmitzer Gemeindewäldchen begrenzt. Zusätzlich zählt noch ein quer durch den Schilfgürtel zum offenen See ziehender baumbestandener Damm bei der biologischen Station zur Probefläche. Das Hinterland besteht im wesentlichen aus intensivst genutzten Weinbaumonokulturen, die manchmal durch Salzlacken (z.B. der Langen Lacke) voneinander getrennt sind. Die Zusammensetzung der Gehölze ist sehr unterschiedlich, meistens ist die Robinie *Robinia pseudoacacia* (Fabaceae) die vorherrschende Baumart, während Pappeln (v.a. P*opulus alba*), Weiden, *wie Salix alba*, *S. cinerea*, die Ölweide *Elaeagnus angustifolia* (Salicaceen) oder Schlehen *Prunus spinosa* (Rosaceae) nur eine untergeordnete Rolle spielen.

Das Gebiet am Westrand des Neusiedlersees umfaßt die Dämme bei Breitenbrunn, Winden, Jois und Neusiedl.

Auf beiden Seiten der Dämme befinden sich ausgedehnte Schilfbereiche, der Damm selber wird vereinzelt von Pappeln *Populus alba* und Weiden, meist *Salix alba* begrenzt.

Sowohl im Gebiet bei Illmitz, als auch an den Dämmen des Westufers wurde eine tägliche Kontrolle im Zeitraum von Mitte Juni bis Anfang August 1992 durchgeführt. Abb. 3 und Abb. 4 zeigen die Verteilung der Nester in den Untersuchungsgebieten.

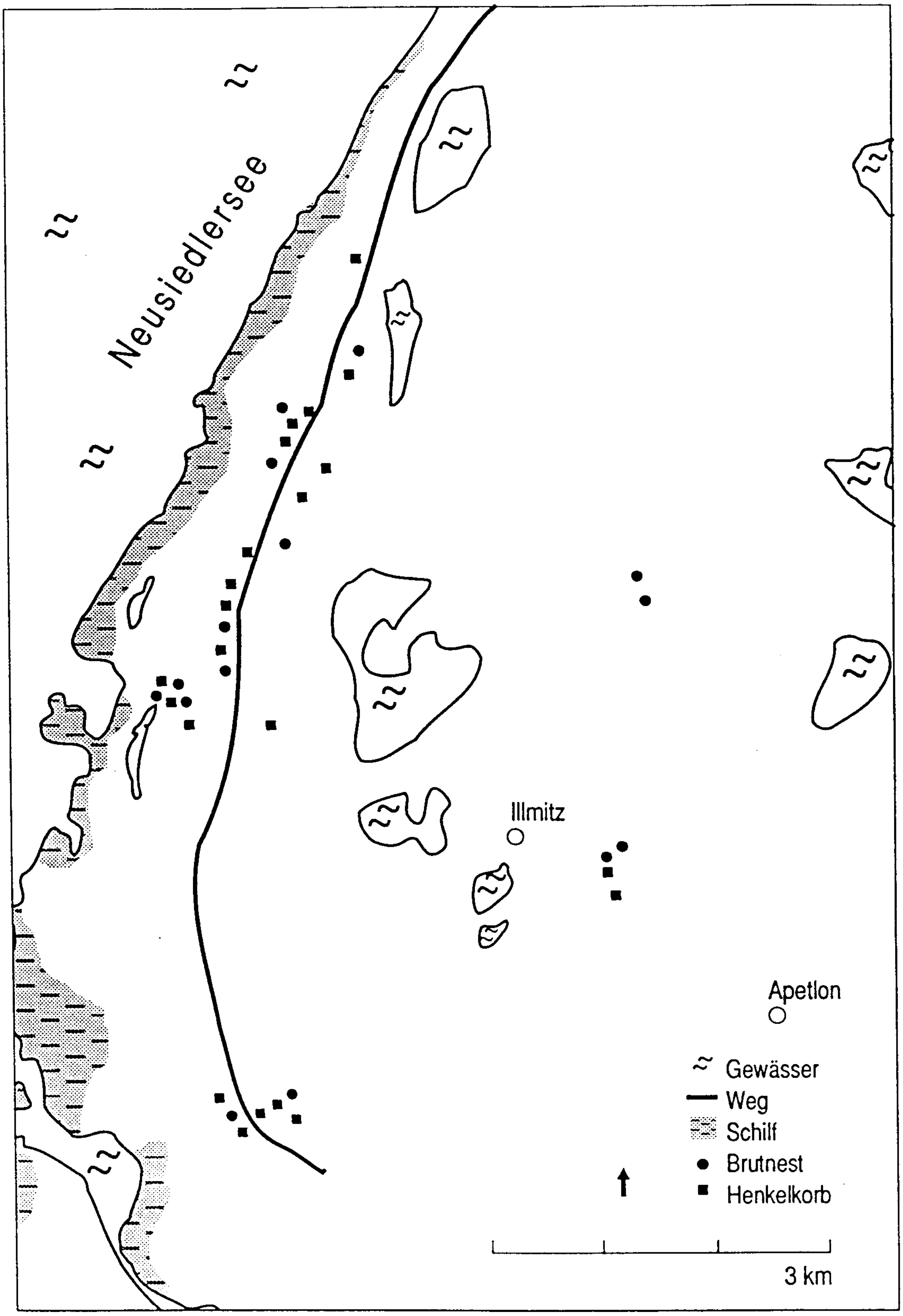


Abb. 3: Verteilung der Beutelmeisennester im Raum Illmitz von Mitte Juni bis Anfang August 1992.

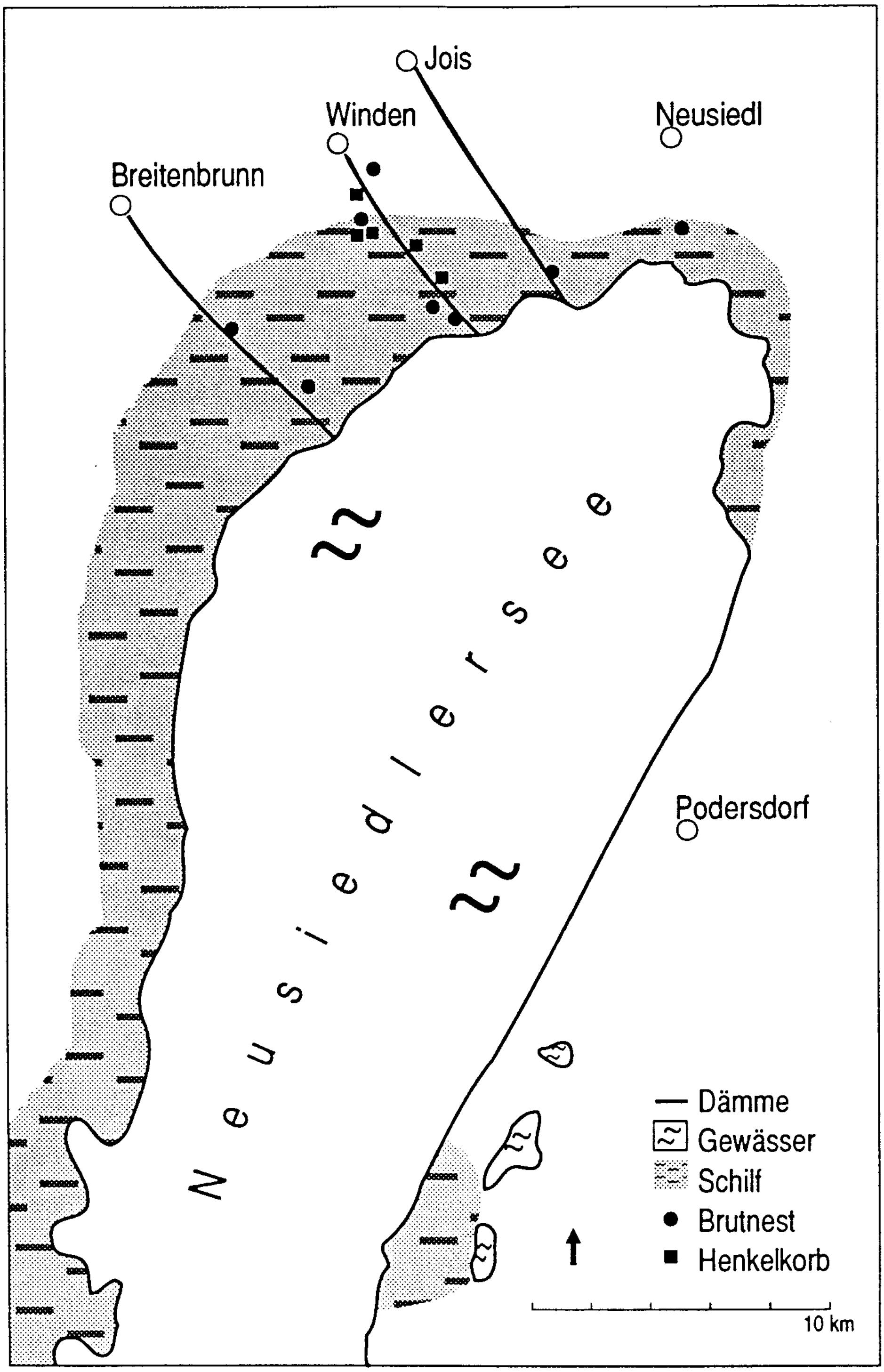


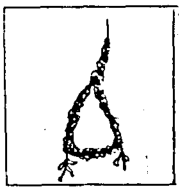
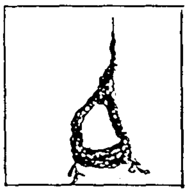
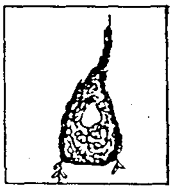
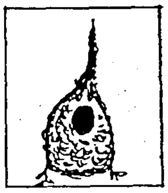
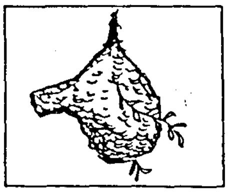
Abb. 4: Verteilung der Beutelmeisennester an den Dämmen des Westufers von Mitte Juni bis Anfang August 1992.

Allgemeine Methoden:

Insgesamt wurden an 77 Nestern 422 Protokolle à 20-Minuten (unterteilt in 30-Sekundenintervalle) aufgenommen, in denen die Aktivität der Individuen am Nest und bis in eine Entfernung von 100 m festgehalten wurde. Die Protokolle waren auf den ganzen Tag verteilt, konzentrierten sich jedoch in den frühen Morgen- und Nachmittagsstunden. Ihre Verteilung auf die einzelnen Neststadien ist in Tab. 2 dargestellt. Voraussetzung für diese Untersuchung war jedoch eine individuelle Farbberingung der Geschlechter.

Mit Hilfe von Japannetzen (6m Länge, Maschenbreite 12mm) und einer Klangattrappe (Walkman und dazugehörenden Boxen) wurden die Vögel gefangen. Als zusätzliches Lockmittel wurden noch ein altes Beutelmeisennest und Watte angeboten. Die Vögel, die in unmittelbarer Nestnähe gefangen wurden, wurden mit einem Aluminiumring der Vogelwarte Radolfzell und einem Plastikfarbring ausgestattet.

Tabelle 2: **Verteilung der Protokolle auf die einzelnen Neststadien** (insgesamt wurden 77 Nester einbezogen)

	Ring	Schaukel	Henkel	fortg. Henkel	Tasche	fertiges Brutnest
						
Anz. d. Nester	9	8	45	25	34	25
Anz. d. Prot./Nest	2±1.2	2±1.4	3±2.6	3±1.9	3±2.5	3±2.3

Literatur

BIRKHEAD, T.R. 1988: Behavioural aspects of sperm competition in birds. Adv. Study Behav. 18: 35 - 72.

- -, ATKIN, L. & MØLLER, A.P. 1987: Copulation behaviour of birds. Behaviour 101: 101 - 138.

BIRKHEAD, T.R. & MØLLER, A.P. 1992: Sperm Competition in birds. Evolutionary Causes and Consequences. Academic Press, Cambridge.

BORGIA, G. 1985a: Bower quality, number of decorations and mating success of males satin bowerbirds (Ptilinorhynchus violaceus): An experimental analysis: Anim. Behav. 33: 266 - 271.

BURKE, T., DAVIES, N.B. BRUFORD, M.W. & HATCHWELL, B.J. 1989: Parental care and mating behaviour of polyandrous dunnocks *Prunella modularis* related to paternity by DNA finger-printing. Nature 338: 249 - 251.

CATCHPOLE, C.K. 1983: Variation in the song of the great reed warbler *Acrocephalus arundinaceus* in relation to mate attraction and territorial defence. Anim. Behav. 31: 1217 - 1225.

COLLIAS, N.E., & VICTORIA, J.K. 1978: Nest and mate selection in the village weaverbird *Ploceus cucullatus*. Anim. Behav. 26: 470 - 479.

EMLEN, S.T. & ORING, L.W. 1977: Ecology, sexual selection and the evolution of mating systems. Science 197: 215 - 223.

FITCH, M.A. & SHUGART, G.W. 1984: Requirements for a mixed reproductive strategy in avian species. Am. Nat. 124: 116 - 126.

FLADE, M., FRANZ, D. & HELBIG, A. 1986: Die Ausbreitung der Beutelmeise (*Remiz pendulinus*) an ihrer nordwestlichen Verbreitungsgrenze bis 1985. J. Orn. 127: 261 - 287.

FORD, N.L. 1983: Variation in mate fidelity in monogamous birds, in: Current Ornithology, Vol. 1. pp. 329 - 351. Plenum Press, New York.

FRANKE, H. 1938: Zi-i-h - die Beutelmeise. Franz Deuticke Verlag, Wien und Leipzig.

FRANZ, D. 1987: Besonderheiten der Brutbiologie der Neusiedlersee - Population der Beutelmeise *Remiz pendulinus*. Ber. biol. Forsch. Inst. Burgenland 63: 103 - 108.

- - 1988c: Wanderungen der Beutelmeise *Remiz pendulinus* während der Brutperiode - Ausdehnung, Häufigkeit und ökologische Bedeutung. Vogelwelt 109: 188 - 206.

- - 1991: Paarungssystem und Fortpflanzungsstrategie der Beutelmeise *Remiz p. pendulinus.* J. Orn. 132: 241 - 266.

FRANZ, D., KORTNER, W. & THEISS, N. 1979: Invasionsartiges Auftreten der Beutelmeise *Remiz pendulinus* im Oberen Maintal und ihre Brutbiologie. Anz. orn. Ges. Bayer 18: 1 - 21.

- - & THEISS, N. 1983: Brutbiologie und Bestandsentwicklung einer farbberingten Population der Beutelmeise *Remiz pendulinus.* Verh. orn. Ges. Bayern 23: 393 - 442.

- - THEISS, N. & GRAFF, H. 1987: Weibchen der Beutelmeise *Remiz pendulinus* brütet in einer Saison zweimal erfolgreich an zwei mehr als 200 km voneinander entfernten Brutplätzen. J. Orn. 128: 241 - 242.

GREIG-SMITH, P.W. 1982: Seasonal patterns of song production by male stonechats (Saxicola torquata). Ornis. Scand. 13. 225 - 231.

HEISLER, I.L. 1981: Offspring quality and the polygyny threshold: A new model for the "sexy son hypothesis". Am. Nat. 117: 316 - 328.

HILL, G.E. 1990: Female house finches prefer colourful males: sexual selection for a condition-dependent trait. Anim. Behav. 40: 563 - 572.

HINDE, R.A. 1952: The behaviour of the great tit (*Parus major*) and some other related species. Behaviour, Suppl. 2: 1 - 201.

JEHL, J.R., JR & MURRAY, B.G., JR. 1986: The evolution of normal and reverse sexual size dimorphism in shorebirds and other birds, in: Current Ornithology, Vol. 3. pp. 1 - 76. Plenum Press, New York.

JENNI, D.A. & COLLIER, G. 1972. Polyandry in the American jacana *Jacana spinosa.* Auk. 89. 743 - 765.

KREBS, J. R. & DAVIES N. B. 1991: Behavioural Ecology: An Evolutionary Approach. Blackwell Scientific Publications, Oxford. 3rd. Edition.

LACK, D. 1968: Ecological adaptations for breeding in birds. Methuen, London.

Mc KINNEY, F., CHENG, K.M. & BRUGGERS, D.J. 1984: Sperm competition in apparently monogamous birds. In: Sperm competition and the Evolution of Animal Mating Systems, R.L: SMITH (ed.). pp. 523 - 545. Academic Press, Orlando.

MOCK, D.W. 1983: On the study of avian mating systems. In: Perspectives in Ornithology. A.H. BRUSH and G.A. CLARK (eds.). pp. 55 - 91. Cambridge University Press, Cambridge.

MØLLER, A.P. 1988: Female choice selects for male sexual tail ornaments in the monogamous swallow. Nature, London 332: 640 - 642.

- - 1990a: Changes in the size of avian breeding territories in relation to the nesting cycle and risks of cuckoldry. Anim. Behav. 40: 1070 - 1079.

- - 1990: Male tail length and female mate choice in the monogamous swallow *Hirundo rustica.* Anim. Behav. 39: 458 - 465.

NISBET, C.F. 1977: Courtship feeding and clutch size in common terns. *Sterna hirundo.* In STONEHOUSE, B., C.M. PERRIS: Evolutionary Ecology. Macmillan, London. pp. 101 - 109.

ORING, L.W. 1982: Avian mating systems. In. D.S. FARNER, J.R. KING & K.C. PARKER (eds.). Avian Biology, Vol. 6: 1 - 92. Academic Press, New York.

PERSSON, O. & ÖHRSTRÖM, P. 1989: A new avian mating system: ambisexual polygamy in the Penduline Tit *Remiz pendulinus.* Ornis Scand. 20: 106 - 111.

SEARCY, W.A. & ANDERSSON M.B. 1986: Sexual selection and the evolution of song. Anual review of ecology and systematics. Am. nat. 17: 507 - 533.

SMITH, S.M. 1988: Extra-pair copulations in black-capped chickadees: the role of the female. Behaviour 107: 15 - 23.

SNOW, D.W. 1958: A Study of Blackbirds. C. Allen and Unwin. London.

TRIVERS, R.L. 1972: Parental investment and sexual selection. In: Sexual Selection and the Descent of Man 1871 - 1971 (Ed. by B. CAMPBELL). pp. 136 - 179. Chicago, Aldine.

VERNER, J. & WILLSON, M.F. 1966: The influence of habitats on mating systems of North American passerine birds. Ecology 47: 143 - 147.

- - 1969: Mating systems, sexual dimorphism and the role of male North American passerine birds in the nesting cycle. Orn. Monogr. 9: 1 - 76.

WEATHERHEAD, P.J. & ROBERTSON, R.J. 1979: Offspring quality and the polygyny threshold: "the sexy son hypothesis". Am. Nat. 113 203 - 208.

- - 1981: In defense of the "sexy son hypothesis". Am. Nat. 117: 349 - 356.

WITTENBERGER, J.F. 1976: The ecological factors selecting for polygyny in altricial birds. Am. Nat. 110: 779 - 799.

- - 1979: The evolution of mating systems in birds and mammals. In: P. MASTER & J. VANDENBURGH (eds.): Handbook of Behavioural Neurobiology, Social Behaviour and Communication. pp. 271 - 349. Plenum Press, New York.

WITTENBERGER, J.L. & TILSON, R.L. 1980: The evolution of monogamy: hypotheses and evidence. A. Rev. Ecol. Syst. 11: 197 - 232.

THE CONFLICT BETWEEN NEST GUARDING AND MATE GUARDING IN PENDULINE TITS (*REMIZ PENDULINUS*)

Abstract

In penduline tits (*Remiz pendulinus*) polygynous males build several very elaborated nests during one breeding season to attract females. The time and effort invested in nest building is related to their mating success. During the breeding season, there is intraspecific competition for nest material resulting in the theft of material from neighbouring nests. The neighbouring males, then experience delays during the period of nest building which in turn decreases male mating success. The thieves benefit by increasing their rate of acquiring nest materials which reduces the effort invested in nest building. There is a negative relationship between the presence of the male near the nest, used as an indicator for nest guarding, and the frequency of nest material theft. In this study we tried to test how nest guarding in males conflicts with their mate guarding behaviour.

Our results show that nest building is costly and nest guarding is an efficient strategy to avoid thieves, but is also costly in terms of a males time budget because it is required for the whole building period. Males, however, spend less time near the nest during the female's fertile phase than during the prefertile period, suggesting that males perform mate guarding to ensure their paternity. As nest guarding is affected by a female's fertile period, a conflict between mate and nest guarding arises. Confronted by this trade-off, males show a preference to perform mate guarding instead of nest guarding.

Introduction

Mate guarding is one of the most effective strategies for males to increase paternity certainty (reviewed in BIRKHEAD & MØLLER 1992). However, this behaviour has been shown to be costly for males in terms of energetic expenditure (ASHCROFT 1976; HOHMAN 1986), reduced food intake (RIDLEY & HILL 1987) and generally as a time consuming activity (GRAFEN 1980; BIRKHEAD & MØLLER 1992). As two different activities cannot be maximized simultaneously, mate guarding may result in a trade-off between the benefits of protecting paternity versus the benefits of other activities. Territorial defense and close mate guarding, for instance, may be difficult for a male to perform simultaneously (SHERMAN & MORTON 1988). In some owls and raptors, males must deliver food during their mates' fertile period (NEWTON 1979). Because intraspecific competition for reproductive opportunities is often intense, nest or territory take-overs or stealing of nest material may occur. Because of these reasons in some colonial breeding species like the common guillemot *Uria aalge* (BIRKHEAD et al. 1985) or the white ibises (FREDERICK 1987), at least one partner has to guard the nest during the fertile period (BIRKHEAD et al.1987). In these cases the possibility of mate guarding during females fertile period depends on how far nest sites are located from resources like food and water which influences how long males have to spent out of the colony due to foraging.

In comparison to most other passerine species, males of the penduline tits (*Remiz pendulinus*), devote a lot of time and energy in the process of constructing elaborate nests. This initial investment seems to influence male's reproductive success in two ways. Firstly, a male advertising a nest in advanced building phases has a higher probability to attract a mate than another male with a nest in an earlier building phase (FRANZ & THEISS 1983). Secondly, upon finishing one nest as quickly as possible, they can earlier attract further females by building additional nests. Theft of nest material has been frequently recorded (FRANZ & THEISS 1983; VALERA 1988). As thefts can delay the progress in nest building we would expect that males should have developed vigilance behaviour to deter thieves. However, efficient nest guarding must be time consuming. Therefore we would expect, especially during females fertile period, that male penduline tits face a conflict between nest guarding and mate guarding (see BIRKHEAD et al. 1987).

In this study we want to examine a) the neccessity and efficiency of male nest guarding b) the occurrence of mate guarding and c) how these behaviours are related in penduline tits. Concerning the importance of nest guarding we examined the relationship between the presence of males near the nest and the incidence of nest material theft. To evaluate the occurrence of mate guarding and to determine if there is a conflict between nest guarding and mate guarding we focused on a) the duration of time that males spent near the nest and near the female during females prefertile and fertile period and b) such events where females depart the nests and the male must actually decide between leaving the nest unguarded and following the female (mate guarding) or remaining near the nest although the female leaves (nest guarding). If it is important to decrease the uncertainty of paternity one would expect that the duration of stay near the female and the number of flights where males immediatly follow their mates should increase during the fertile period.

Methods

Birds were mist-netted and individually colour ringed during the breeding season 1992 in two different sites about 60 km from Vienna, a wet forest area along the river March and the region around Lake Neusiedl. Behavioural observations were done throughout a day for 20 minute observation periods using time sampling in 30 sec intervals. Medians ($\tilde{x}$) and interquartile ranges (iqr) are given.

We measured nest building activity, frequency of thefts and the time taken by collectors and thieves to get a load of nest material. We classified the flights to obtain nesting material in several distance classes from the nest. We calculated the average growth rate/day of 17 nests as a measure of the amount of material builders were able to gather. The average weight losses/day of material stolen by thieves was calculated using the weights of 4 nests before destruction and the time needed by thieves to destroy them completely.

In general the prefertile and fertile period were distinguished by the start of egg-laying. Because it is known that start of egg-laying is correlated with completion of egg chamber (see FRANZ & THEISS 1983) we seperated the two periods according to this nest building phase (prefertile before and fertile after completion of the egg chamber and starting the entrance tube) in those cases where we could not reach the nest. In both periods the male's trade-off between nest guarding and mate guarding were compared. As a measure of nest guarding behaviour we considered the time that males spent near the nest (within a radius of 10 m). As mate guarding activity we measured the time that both sexes spent together (within a radius of 10 m) near (<10 m) and far from the nest (>10 m).

The statistical tests used were non parametric according to SIEGEL (1956). A Craddock and Flood Chi^2 approximation (LIENERT 1986) was used to test the difference in theft activity during different breeding phases (unmated, prefertile, fertile and incubation phase). To compare the males' trade-off between the prefertile and fertile period we used a conditional binomial exact test (RICE 1988) because this test, in contrast to Fishers exact test, accommodates different levels of a priori information about the underlying probabilty. To reduce the effect of outliers and the deviation from normality robust regression analyses (HAMILTON 1992) were used to examine the relationship between a) nest guarding and frequency of thieves and b) the time both sexes spent far from the nest during the prefertile and fertile period.

Results

Males required about 19 days to finish a nest (FRANZ et al. 1979; VALERA 1988). Males invested about 15 % of their time ($\tilde{x}$=4.9, iqr=2.4-9.1 intervals/20 min of 32 nests) constructing the nests and 10.1 % of time gathering the material ($\tilde{x}$=4.05, iqr=1.3-5 intervals/20 min of 32 nests). Therefore, overal they devote about 25 % of their time in nest building activities. Males usually collected nest material from areas surrounding the nest (Fig. 1), or they "stole" it from other nests in the vicinity.

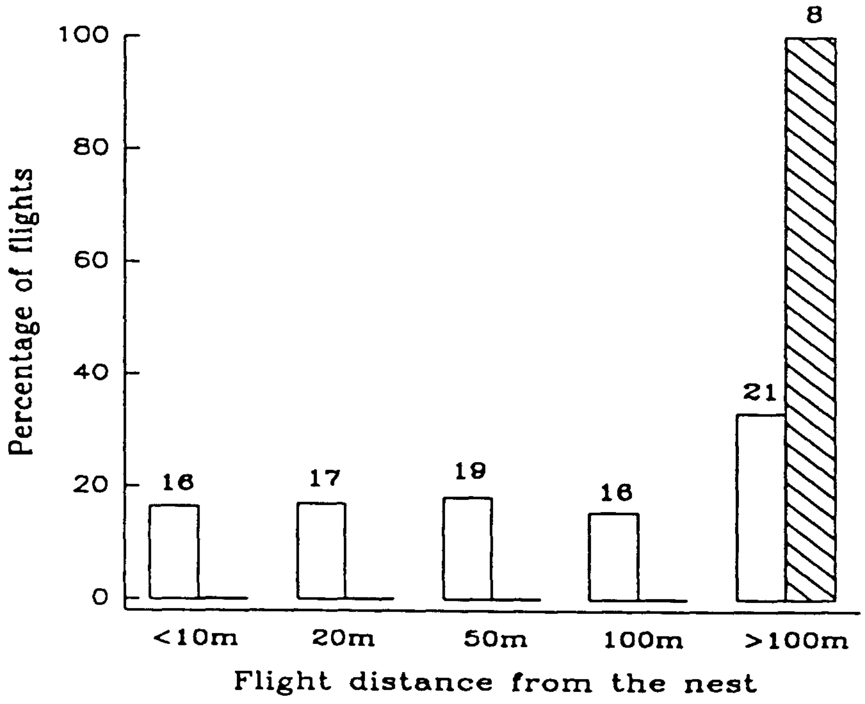


Fig.1: Distance of flights to gather material of collectors (open bars; no. of males: 39; no. of flights: 168) and thieves (hatched bars, no. of males: 8; no. of flights:14). The number of males in each distance class is given on the top of each bar.

Comparing the collecting time for material (including travel time), thieves used less time to steal material from unguarded nests than collectors to gather it from the surroundings (Mann-Whitney U test, z=3.0, p<0.001, Fig. 2) and additionally, thieves can remove material from a nest at a significantly faster rate than a collector can construct a nest (z=3.0, p<0.001). The actual time thieves require to remove material from a foreign nest was very low ($\tilde{x}$=0.28, iqr=0.23-0.8 intervals/20 min of 13 nests).

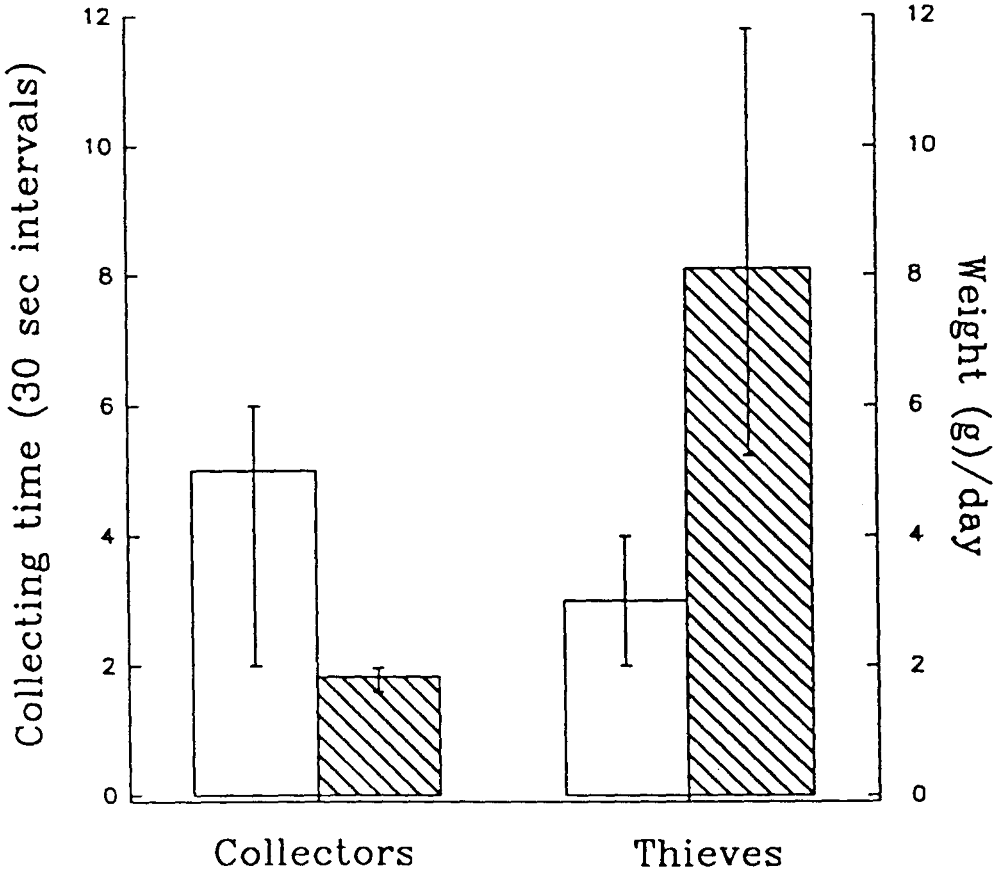


Fig.2: Comparison of the time (open bars) collectors (males acquiring material from natural resources) and thieves (males acquiring material from other nests) require for a given travel distance (>100 m) and comparison of the amount of material (hatched bars) collectors and thieves acquire per day. Median and interquartiles are given for 30 sec intervals/20 min observation periods and weight in gramm/day.

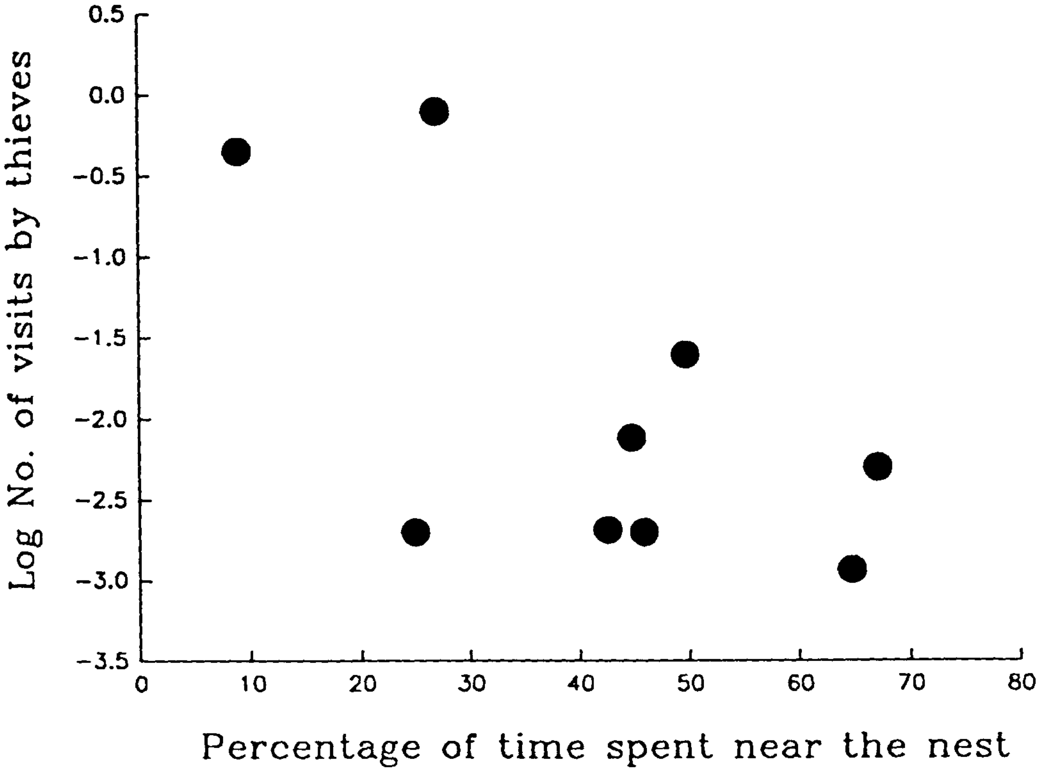


Fig.3: Relationship between nest guarding activity (% of time males spent near the nest, within 10 m) and the mean frequency of thefts (log transformed data) during 20 min observation periods.

In figure 3, one can see that the average time males spend near the nest (< 10 m) varies considerably and this is negatively related to the frequency of observed thefts (r=-0.76, p=0.018, n=9 nests). Comparing different breeding phases (unmated, prefertile, fertile and incubation phase), there was no difference in intraspecific theft activity (Craddock-Floods chi2 approximation, Chi2=4.44, p>0.1). But males spent less time near the nest during the females' fertile phase ($\tilde{x}$=12.29, iqr=5.6-19.5 intervals/20 min of 28 nests) than during the prefertile phase ($\tilde{x}$=20.3, iqr=15.5-27.5 intervals/20min of 32 nests; Mann-Whitney U test, z=3.47, p<0.001).

We found no difference in the time both partners spent together near the nest (within 10 m) between the prefertile and fertile phase (Mann-Whitney U test, z= 0.99, p>0.1). However, in the distance class between 10 and 50 m away from the nest, they spent singnificantly more time together during the fertile than during the prefertile period (Mann-Whitney U test, z=2.02, p<0.05). It is difficult to obtain data on mate guarding farther than 50 m from the nest, but there was a positive relation between the time both partners were away from the nest (>50 m) during the fertile phase (r=0.57, p<0.001, n=32 nests) but not during the prefertile phase (r=0.35, p>0.05, n=28 nests) (Fig. 4).

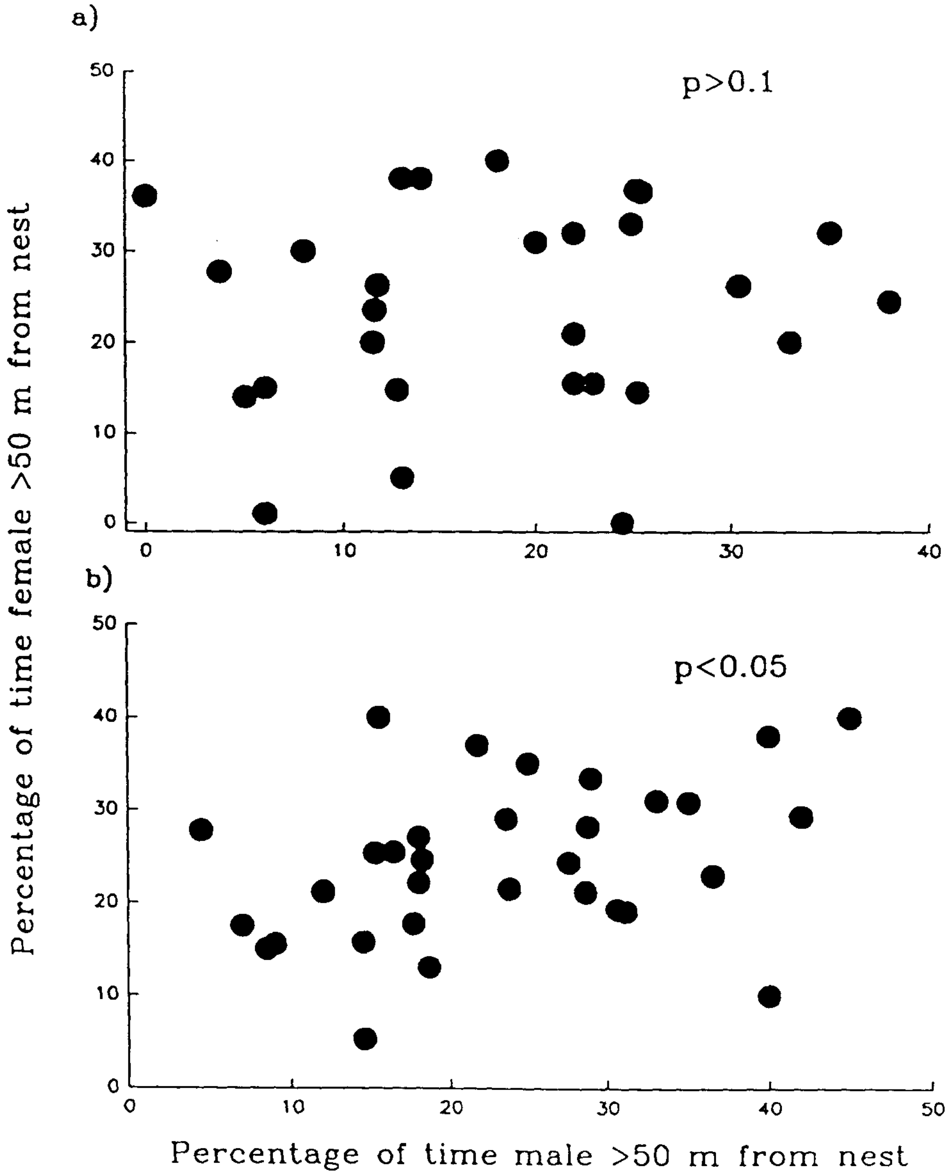


Fig.4: Relationship between the percentage of time males and females stay further than 50 m from the nest during the prefertile (a) and the fertile phase (b). Mean number of 30 sec intervals/20 min observation periods are given.

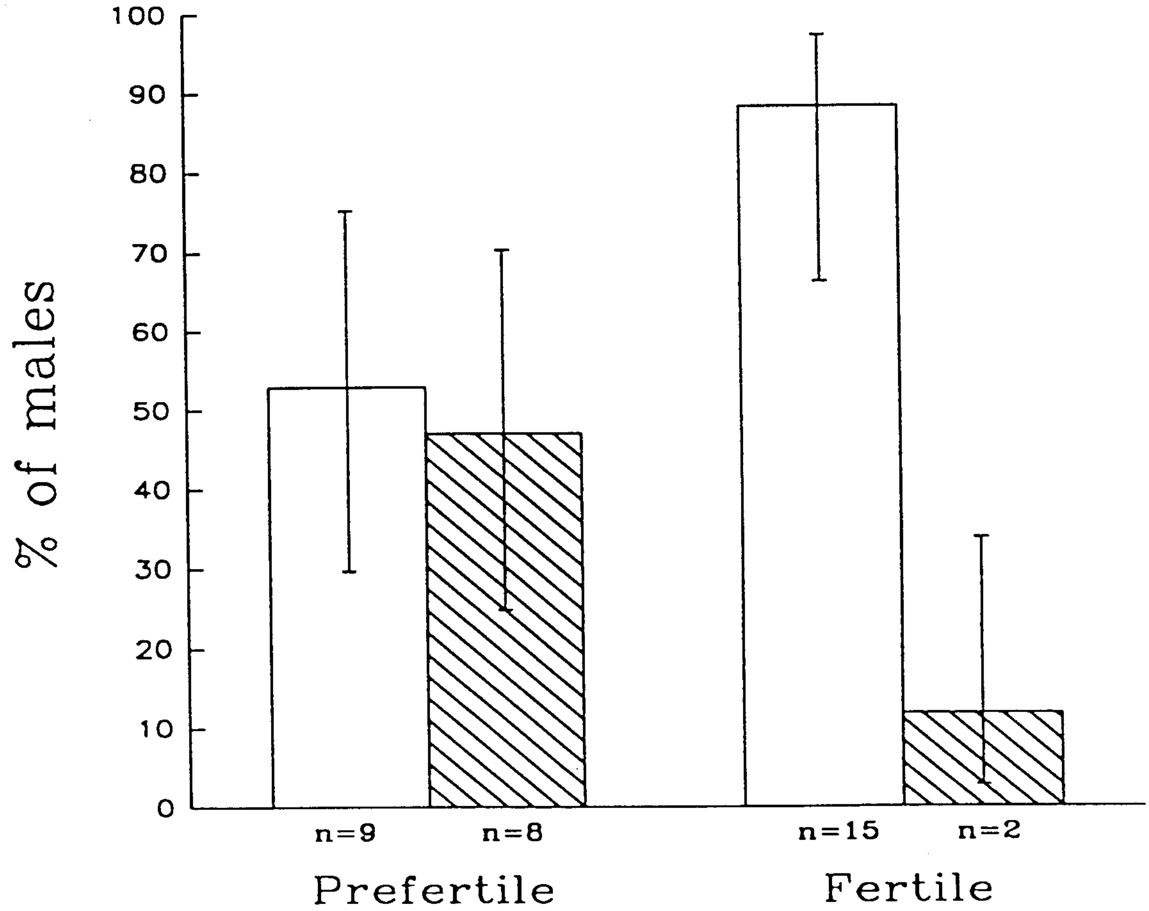


Fig.5: Percentage of males (±confidence limits) which follow the female (open bars) and stay at the nest (hatched bars) during the prefertile and fertile phase.

Finally, figure 5 shows the outcome of such special situations, where males have actually to decide to stay near the nest or to depart with their mate. In the fertile period males accompanied their mates when the mate departed the nest site significantly more often than during the prefertile period (Conditional binomial exact test, $p<0.001$). The trade-off decision made by males is nevertheless in conflict, as evidenced by the fact that even males who performed mate guarding during the female's fertile phase, in at least 5 out of 31 (16 %) such situations, they stayed near the nest.

Discussion

The results suggest that nest building activity in penduline tits require a substantial proportion of males time budget (Fig. 2). In penduline tits and other species, like the fan-tailed warbler *Cisticola juncidis* (UEDA 1984) and the village weaver *Ploceus cucullatus* (COLLIAS & COLLIAS 1984), progress in nest building depends largely on the availability of material in areas surrounding the nest (unpubl.data). In addition, intraspecific competition involving the theft of nest material can delay the process of nest building (see also CULLEN 1957; COLLIAS & COLLIAS 1984). The results show that theft activity, even if it involves long distance flights (see FRANZ & THEISS 1983; VALERA 1988), is very efficient because males following this strategy, need less time to acquire material (Fig. 2). Additionally the time taken to collect a load of nest material also reflects how long the nest would be left exposed to other thieves. This stealing behaviour, however, forces nest owners to safeguard their nests from demolition. This may be reflected in the fact that males stay up to 70 % of their time near the nest (see Fig. 3) although they require only 15 % of the time in building. Unlike other species (CULLEN 1957; reviewed in COLLIAS & COLLIAS 1984), nest guarding prior to incubation in penduline tits is almost exclusively performed by the male. The importance of nest guarding in this species is supported by additional evidence: a) many other species like goldfinches *Carduelis carduelis*, olivaceous warblers *Hyppolais pallida* (VALERA 1988), golden orioles *Oriolus oriolus* and reed warblers *Acrocephalus scirpaceus* (FRANZ & THEISS 1983) have been observed to remove nest material from penduline tit nests, b) there is a high rate of female desertion before egg-laying which may be due to harassment by theft activity (unpuplished data) and c) thefts occur during the whole nesting period.

Although the frequency of thefts did not vary between different breeding phases males spent less time guarding the nest during the females' fertile phase which may reflect a conflict between mate and nest guarding behaviour. Comparing the time both partners stay together during the female's prefertile and fertile phase, no differences were found near the nest. This is may be a consequence of the fact that at this distance probably males are able to perform nest guarding and mate guarding at the same time.

In contrast, far away from the nest mate attendance significantly increased in the fertile period. Finally, in situations where males must choose between staying near the nest or following the female, males, in general, prefer to follow their mates in particular during the females' fertile period. This trade-off has already been described in situations where competition is particularly intense (i.e. in colonially breeding birds), where nest guarding by males is so important that it overrides the value of mate guarding for males (BIRKHEAD et al. 1987; WAGNER 1992). Our results, suggest that the decisions of males are not clear cut. Sometimes, however, they perform nest guarding even during the females fertile phase, which may suggest that a male's trade-off decision is situation dependent. This trade-off could be influenced by factors like the males' information about the females' fertile states, the time of day (the probability of fertilization is higher after egg-laying see BIRKHEAD & MØLLER 1992), the probability of future thefts as estimated by the number of preceeding thefts or the number of neighbours, or food constraints (FREDERICK 1987).

Our results suggest that nest guarding in this species competes for a male's time and energy requirements, epecially with mate guarding behaviour.

Do males therefore use other strategies to ensure paternity certainty? Frequent copulation, which is often cited as an alternative paternity guard (MØLLER & BIRKHEAD 1991) seems to be unlikely in penduline tits. Copulations seem to be rare (unpupl.data from field observations and from aviary observations E.Thaler pers.comm.) and the males' cloacal protuberances are small, which makes sperm competition through frequent copulations unlikely in this species (NAKAMURA 1990; BIRKHEAD et al. 1991). Territoriality as a kind of paternity guard (BIRKHEAD & MØLLER 1992) also seems unlikely. This was tested using playback experiments, particularly during the females' fertile phase (unpubl.data), and revealed a weak defense reaction, near the nest and in the immediate surroundings (see also FRANKE 1937; FRANZ & THEISS 1983). In addition, it appears that mate guarding and territorial defense cannot be performed simultaneously (see SHERMAN & MORTON 1988).

Do males need do guard their mates? In penduline tits only a low proportion of males incubate and feed the young (FRANZ 1991). As Rhijn (1984, 1991) stated, intensive mate guarding should occur in species with high male parental investment, so the question arises if there is any reason for intensive mate guarding in penduline tits. Because of the strong initial investment in nest building which requires about 19 days of work and which is necessary for every nesting attempt, we would expect that males should be highly interested in insuring paternity.

Male penduline tits appear to be left with the dilemma of mate versus nest guarding behaviour. The best solution may be to balance these behaviours depending on the state of the female, frequency of thefts and relative costs of nest building. Because efficient mate guarding seems to be unlikely, one would expect a general high rate of extra-pair fertilizations (EPF's). To elucidate this trade-off more information is needed on a) the degree of sperm competition in this species (EPF rate) and b) how ecological factors like population density, seasonal variation in operational sex ratio, resources and intraspecific competition modulate male decisions.

Literature

ASHCROFT, R.E. 1976: A function of the pairbond in the common eider. Wildfowl 27, 101-105.

BIRKHEAD, T.R., JOHNSON, S.D. & NETTLESHIP, D.N. 1985: Extra-pair matings and mate guarding in the common murre *Uriaa aalge*. Anim. Behav. 33, 608-619.

BIRKHEAD, T.R., ATKIN, L. & MØLLER, A.P. 1987: Copulation behaviour of birds. Behaviour 101, 101-138.

- -, HATCHWELL, B.J. & DAVIES, N.B.1991: Sperm competition and the reproductive organs of the male and female dunnock (*Prunella modularis*). Ibis 133, 306-311.

- - & MØLLER, A.P. 1992: Sperm Competition in Birds. Evolutionary Causes and Consequences. Academic Press, Cambridge.

COLLIAS, N.E. & COLLIAS, E.C. 1984: Nest Building and Bird Behaviour. Princeton Univ. Press, Princeton.

CULLEN, E. 1957: Adaptions in the Kittiwake to cliff nesting. Ibis 99, 275-302.

FRANKE, H. 1937: Aus dem Leben der Beutelmeise. Beitr. Fortpfl. Biol. Vögel 13, 85-94.

FRANZ, D. 1991: Paarungssystem und Fortpflanzungsstrategie der Beutelmeise (*Remiz p. pendulinus*). J. Orn. 132, 241-267.

- -, KORTNER, W. & THEISS, N. 1979: Invasionsartiges Auftreten der Beutelmeise *Remiz pendulinus* im Oberen Maintal 1978 und ihre Brutbiologie. Anz. orn. Ges. Bayern 18, 1-21.

- - & THEISS, N. 1983 : Brutbiologie und Bestandsentwicklung einer farbberingten Population der Beutelmeise *Remiz pendulinus*. Verh. orn. Ges. Bayern 23, 393-442.

FREDERICK, P.C. 1987: Extra pair copulations in the mating system of White Ibis *Eudocimus albus*. Behaviour 100, 170-201.

GRAFEN, A. 1980: Opportunity costs, benefit and the degree of relatedness. Anim. Behav. 28, 967-968.

HAMILTON, L.C. 1992: Regression with graphs: a second course in applied statistics. Brooks and Cole, Belmont, California.

HOHMAN, W.L. 1986: Changes in body weight and body composition of breeding ring-nacked ducks (*Aythya collaris*). Auk 103, 181-188.

LIENERT, G.A. 1986: Verteilungsfreie Methoden in der Biostatistik. Band 1, Anton Hain, Meisenheim.

MØLLER, A.P. 1992: Sperm Competition in Birds. Evolutionary Causes and Consequences. Academic Press, Cambridge.

- - & BIRKHEAD, T.R. 1991: Frequent copulations and mate guarding as alternative paternity guards in birds: a comparative study. Behaviour 118, 170-186.

NAKAMURA, M. 1990: Cloacal protuberance and copulatory behaviour of the Alpine accentor *Prunella collaris*. Auk 107, 284-295.

NEWTON, I. 1979: Population Ecology of Raptors. Poyser, Berkhamsted.

VAN RHIJN, J.G. 1984: Phylogenetical constraints in the evolution of parental care strategies in birds. Neth.J.Zool. 34, 103-122.

- - 1991: Mate guarding as a key factor in the evolution of mating systems in birds. Anim. Behav. 41, 963-970.

RICE, W.R. 1988: A new probability model for determining exact p-values for 2 x 2 contingency tables when comparing binomial proportions. Biometrics 44, 1-22.

RIDLEY, M.W. & HILL, D.A. 1987: Social organization in the pheasant *Phasanius colchicus*: harem formation, mate selection and the role of mate guarding. J. Zool. Lond. 211, 619-630.

SHERMAN, P.W. & MORTON, M.L. 1988: Extra pair fertilizations in mountain White-crowned Sparrows. Behav. Ecol. Sociobiol. 22, 413-420.

SIEGEL, S. 1956: Non-parametric statistics for the behavioral sciences. McGraw-Hill, New York.

VALERA, F. 1988: Expansión y Biología de Reproducción de *Remiz pendulinus* en el Valle del Guadalquivir. D. Phil. Thesis, Univ. of Granada, Granada.

UEDA, K. 1984: Successive nest building and polygyny of Fan-tailed warblers *Cisticola juncidis*. Ibis 126, 221-229.

WAGNER, R.H. 1992: The use of extrapair copulations for mate appraisal by razorbills, *Alca torda*. Behav. Ecol. 2, 198-203.

MATE CHOICE IN PENDULINE TITS (*REMIZ PENDULINUS*): THE IMPORTANCE OF NEST QUALITY

ABSTRACT

Among penduline tits a high proportion of males are polygynous, some males are monogamous and a few remain unmated throughout the whole breeding season. Penduline tits are non-territorial and perform uniparental care. Males try to attract their mates with elaborate pendulous nests. We therefore expected that nests quality may be important in mate choice. To determine which cues females use for choosing among potential mates we examined the quality of males (morphological and behavioural attributes), the habitat and the nest size.

This study revealed that females of this species do not choose their mates on the basis of phenotypical or behavioural features, but on the basis of nest size. Experiments on nest insulation revealed that females benefit directly by choosing a "good" nest.

INTRODUCTION

The basic approach in studies on mate choice is to find out which cues females use to choose among potential mates and how these cues correlate with future benefits for the female.

In general, females may choose a mate according to territory characteristics (i.e. quality) (LENINGTON 1980, ALATALO et al. 1986) or for phenotypic attributes (BORGIA 1987, HILL 1990). The situation is complicated by male-male competition for territories attractive to females, because there may be a high correlation between male quality and territory quality (WITTENBERGER 1979, HEISLER 1981, REID et al. 1990).

Concerning male quality, most studies focuse on a) morphological features, like colourful plumage or other sexual attributes which lead to the evolution of extravagant male ornamentation (ANDERSSON 1982) and b) male mating skill's. In this context song intensity (REID 1987) as well as song complexity (CATCHPOLE 1980, SEARCY 1988, GREIG-SMITH 1982) are suggested to function in mate choice. Particularly in lek species like the white-throated manakin *Corapipo gutturalis* (PRUM 1985) or the ruff *Philomachus pugnax* (VAN RHIJN 1991) intensity and types of courtship display are important. However, male quality may also be reflected in other features like the size of gifts or nest building skills. For instance, in bowerbirds, male quality is empasized by by presentation of a decorated bower during the courtship display (COLLIAS & COLLIAS 1984). This may reflect male quality but has no direct benefits for the female because bowers are not used for nests and males do not engage in nest construction later on. In other species, mates are attracted by a display of nest sites (COLLIAS & VICTORIA 1978) or by more or less completed nests. A nest may not only indicate male quality, but females could benefit directly from choosing a high quality nest (COLLIAS & COLLIAS 1984). It is known that avian embryos develop best in a relatively warm and stable environment (WHITE & KINNEY 1974), hence certain features of a nest may influence the thermal environment of the eggs. Pendulous nests are especially exposed to wind, precipitation and other adverse environmental conditions. Therefore one would expect that thermal insulation is an important determinant for nest quality.

This study on penduline tits examines the role of nest quality for female choice. In this species, males construct elaborate pendulous nests (FRANZ & THEISS 1983) to attract females. A high proportion of males are polygynous (between 60% and 80%), some are monogamous and a few males remain unmated throughout the whole breeding season (FRANZ 1991, PERSSON & ÖHRSTRÖM 1985). Penduline tits are non territorial and only few males provide parental care. So we would expect that the quality of habitat surrounding the nest and the male's prospensity to invest in parental care are not important for mate choice. As female care without male assistance is the rule, thermal insulation of the nest may increase the time a female can leave eggs or chicks unattended for gathering food.

To examine which factors may actually influence female choice we simultaneously studied the quality of males (considering both morphological and behavioural parameters), nest site quality, and nest quality on the basis of variation in mating succes among males. Additionally we examined the direct benefits females can acquire from a "good" nest.

METHODS

The study was conducted during the breeding season 1992 in two different sites about 60 km from Vienna, at Lake Neusiedl in the Illmitz region (47°46'N, 16°48'E) and a wet forest along the river March near Marchegg (48.16 N, 16.57 E). Birds were mist-netted and individually colour ringed.

To examine the role of physical attributes the mask lenght and width, wing length, weight and fat deposits were measured and later compared with the male's mating success.

To estimate the rate of female visits and male mating success, behavioural observations were made throughout the day using time sampling at 30 seconds intervalls for 20 minute observation periods. To avoid errors due to visits from sporadic females, mating success was defined as a male chosen by a female only in those cases where egg-laying occured.

During the mating period, males use a certain call note to attract potential mates (see FRANZ & THEISS 1983). Therefore we used the call note frequency per 30 sec interval as a measure of a male's courtship intensity. These data were collected for three days on average for each nest during the intermediate nest building state (day 5 to day 10 after nest initiation).

Nest site quality was determined by scoring the characteristics of the surrounding nest vegetation in eight 100 m transects starting from the nest. Along these transects we visually estimated the component covered by the main vegetation types (reed, willows, poplars, black locusts, meadows, grassy scrub, bushes and stinging nettles).

Nest quality was examined using two measures: 1) Nest size: as females choose their mates during an intermediate building state (Henkelkorbphase, see FRANZ et al. 1979, FRANZ & THEISS 1983) nest size is probably the only feature they can use. Nest initiation starts with a ring which correlates well with nest size. This parameter does not change during nest completion and is therefore a valid measure for the intended comparison. 2) Nest thickness: thickness of the nest bottom in completed nests was measured by inserting a needle into the center of the egg-chamber to calculate the distance between bottom and egg-chamber.

Additionally, the thermal insulation property of the nests was measured in a laboratory experiment. A thermistor probe inserted into a wax-filled penduline tit egg was monitored in different nests while a second probe measured the environmental temperature. Each nest was heated to 40 degrees Celsius in an incubator, the starting temperature being 20 degrees Celsius. Both the raise (during one hour) and the drop of the egg temperature (during 20 minutes) was registered in 10 sec intervals. Nests were ranked according to size and thickness of their bottom, whereby the three largest and the three smallest nests were used for these measurements.

RESULTS

Analysis of male attributes

For this purpose males were divided into three classes. a) Unmated males (UM): males without any mate throughout the whole breeding period, b) monogamous males (MM): one successful breeding attempt with one female and c) polygynous males (PM): successful breeding attempts with more than one female.

When morphological differences between the sexes were compared we found that the mask of males' was about 2.3 mm greater in width (Mann-Whitney U test, $p<0.001$, Tab. 3). But, males are in general 2 g lighter than females (Mann-Whitney U test, $p<0.001$, Tab. 3) and these weight differences between sexes increased from unmated (Mann-Whitney U test, UM: $\bar{x}=1.8$ g, $p=0.011$) to mated males (MM: $\bar{x}=2.2$ g, $p=0.003$ and PM: $\bar{x}=2.1$ g, $p=0.001$). However, concerning phenotypic variation among males with differing mating success (UM, MM and PM males), we found no significant differences in any of their morphological features (Tab. 3). There seems to be only a weak difference in wing length between unmated and mated males (MM and PM).

Analysis of courtship intensity

To evaluate the importance of male mating displays we compared calling rates for the same three male categories (UM, MM and PM). The results revealed no difference in the frequency of calling (mean number of call notes/interval (±SD), UM: 3.1 (±0.76), MM: 2.6 (±1.44) and PM: 4.7 (±1.82); Kruskal-Wallis-Test, $p=0.411$, $n=6, 6, 7$).

TABLE 3: Morphological parameters for females and males with different mating success. Significance values (p) for a multiple comparisons test (Kruskal-Wallis test) are given for three male categories. The median, first and the third quantiles in parenthesis, are given.

	mask length	**mask width**	**wing length**	**weight**	**fat**	**n**
females	14.7 (12.3-16.2)	6.4 (6.2-6.6)	54.5 (54.0-56.0)	10.9 (9.9-11.8)	1.0 (0.0-1.0)	8
unmated	15.9 (15.4-16.6)	7.7 (6.3-10.3)	55.0 (53.5-55.5)	9.1 (8.7-9.5)	0.0 (0.0-1.0)	4
monogamous	15.5 (15.0-16.8)	9.5 (7.0-10.0)	56.0 (53.0-57.0)	8.7 (8.7-8.9)	0.0 (0.0-0.0)	6
polygynous	15.6 (14.8-16.9)	8.6 (7.6-9.3)	56.0 (54.4-57.0)	8.9 (8.7-9.29)	0.5 (0.0-1.0)	12
p-value	0.81	0.554	0.551	0.714	0.385	

Analysis of nest site features

Males built their pendulous nests on the extreme outer section of tree crowns (mainly willows and poplars) at a height of 6 m with a range of 2-20 m, sometimes suspended over water. The habitat surrounding the nests was diverse. Due to strong habitat differences especially between our two study areas (see Table 1), we analysed the respective data separately.

To evaluate the importance of nest site quality for female choice, males were categorized as a) unsuccessful males (males never chosen) (US), b) males chosen but females deserted before start of incubation (SD) and c) males chosen and females incubated (SI). As habitat importance should generally decrease with increasing distance from the nest, habitat features surrounding the nest site were originally compared for 50 m and between 50 and 100 m distance from the nest. Because there was no differences ($p>0.5$) using a discriminant analysis for the two distance classes (50 m and >50 m,≤100 m), the data were lumped and a stepwise discriminant analysis was used to compare habitat availability within 100 m around the nest for the three male categories (US, SD and SI males). This analysis was done with two sets of habitat parameters, one for nest material and nutrition and one including all parameters. It is known that some resources, such as reed, willows, poplars and grassy scrub may be important for nest material (see LÖHRL 1981, VALERA 1988) and reed, willows and poplars may be important food resources (see FRANZ & THEISS 1983, FRANZ et al. 1979).

However, in neither study site did a discriminant analysis show a significant difference for the male categories (US, SD and SI, Tab. 4). This was also the case if we considered those habitat variables which could be useful as food or nest material resources (Illmitz, $p>0.05$; Marchegg, $p>0.3$) separatly.

TABLE 4: Habitat composition≤100 m from nests of males with different mating success: SI males (chosen and females incubated), SD males (chosen but females deserted prior to incubation) and US males (never chosen by females). For each habitat, the mean, univariate F- and p-values and the correlation coefficients of these variables for the discriminant factors I and II for a) Illmitz and b) Marchegg, are given.

a)

	Male categories						
	SI	**SD**	**US**	**I**	**II**	**F-value**	**p-value**
Variables	(n = 8)	(n = 5)	(n = 12)				
reed	21.9	15.9	26.7	-0.22	-0.03	0.30	0.74
willows	4.8	6.2	1.5	0.34	-0.09	0.77	0.52
poplars	6.9	3.3	7.9	-0.24	-0.13	0.40	0.67
meadows	16.8	23.5	19.9	0.07	0.27	0.26	0.77
grassy scrub	10.3	1.8	0.9	0.22	-0.84	3.29	0.05 *
bushes	0.6	1.0	1.1	-0.09	0.28	0.30	0.75
water	0.0	0.3	2.5	-0.40	0.33	1.49	0.24
vineyards	8.2	6.8	9.0	-0.10	-0.02	0.06	0.94
black locust	6.5	18.3	5.7	0.38	0.32	1.31	0.28
edges	1.7	1.5	1.5	0.09	-0.30	0.35	0.71
nests	0.5	0.2	0.4	-0.20	0.33	0.54	0.59

b)

	Male categories						
	SI	**SD**	**US**	**I**	**II**	**F-value**	**p-value**
Variables	(n = 7)	(n = 7)	(n = 13)				
reed	2.3	18.8	14.2	-0.48	-0.19	1.71	0.20
willows	22.6	13.9	18.7	0.37	-0.03	0.90	0.57
poplars	3.1	9.4	1.7	-0.38	0.49	2.00	0.16
meadows	4.0	19.8	16.3	-0.64	-0.32	3.73	0.04 *
grassy scrub	9.9	4.6	4.6	0.24	0.22	0.52	0.60
bushes	2.9	2.1	0.0	0.09	0.49	0.99	0.61
water	17.9	7.7	15.4	0.39	-0.17	1.12	0.34
nettles	10.1	1.0	10.8	0.42	-0.42	1.94	0.16
edges	2.2	1.4	1.9	0.58	-0.10	2.47	0.10
nests	0.0	0.4	0.4	-0.50	-0.42	2.34	0.12

Nest quality

Concerning nest quality, we found significant differences in nest size between the three male categories (Kruskal-Wallis test, p=0.0001). A multiple comparison test between the single categories as an extension of ZAR (1984) showed that nests with an incubating female were significantly larger than those which were deserted (Mann-Whitney U test, p<0.001) or which contained no egg at all (p<0.001). Comparing the thickness of the bottom between the three male categories also revealed significances (Kruskal-Wallis test, p=0.0001). Using a multiple comparison test between we could specify that these differences are mainly due to the fact that SI males had nests which were significantly thicker at the bottom than nests of SD males (p=0.01, Fig. 6). But there are no differences in the nest size of US and SD males (p>0.6, Fig. 6).

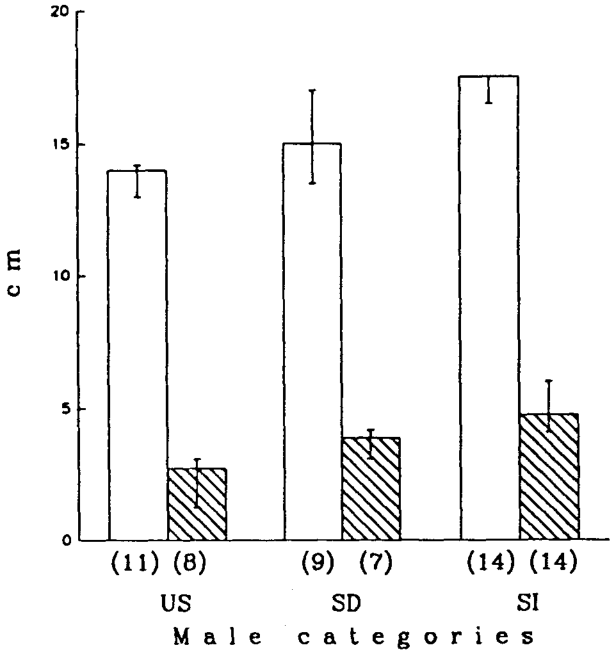


Fig. 6: Nest size (open bars) and thickness of nest bottom (hatched bars) of males with different mating success: US males (never chosen by females), SD males (chosen but females deserted prior to incubation) and SI males (chosen and females incubated). Medians and interquartiles are given. The number of nests is given in parenthesis.

Additionally in figure 7 one can see that this two parameters, the thickness of the bottom and the size of the nest, are positively correlated (r=0.55, p=0.0005).

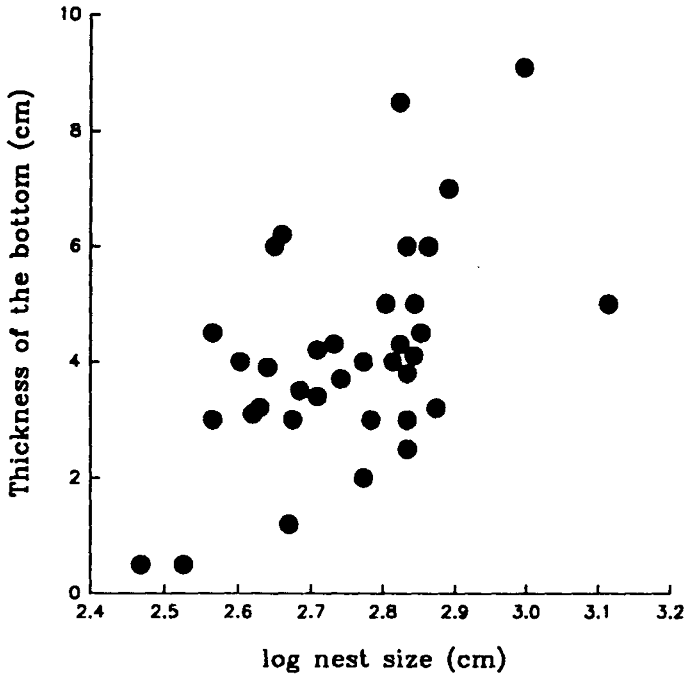


Fig. 7: Correlation between nest size (log transformed data) and thickness of nest bottom (n=36).

Are there benefits by choosing a high quality nest ?

To evaluate if there is any direct advantage by choosing a larger and thicker nest we investigated differences in the insulation capacity of large and small nests. A t-test was applied for parallelism of the slope and the common intercept (KLEINBAUM & KUPPER 1978). For linearity of the data (see Fig.8), time was log transformed and temperature differences (Δt) were square-root transformed.

Comparing the three largest and the three smallest nests the raise (during one hour) and drop of the egg temperature (during 20 min) was about 0.3°C to 0.4°C degrees per minute faster in smaller nests than in larger ones (Fig. 8, for the raise: T=3.08, p<0.01 for the drop: T=1.9, p<0.01 of the egg temperature). That larger nests can hold egg temperature longer is also indicated by the different intercepts (for the raise: T=3.79, p<0.01, for the drop T=3.379, p<0.01 of egg temperature).

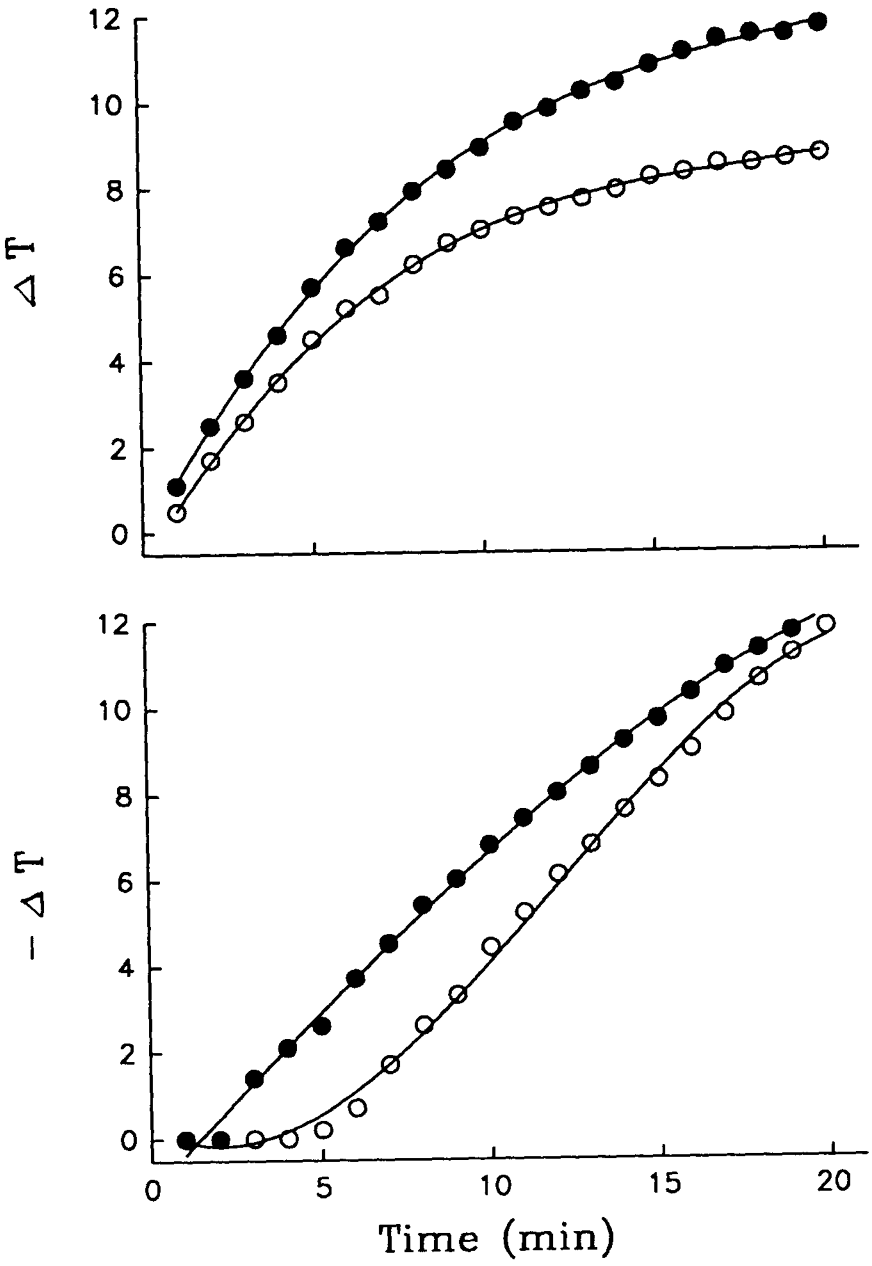


Fig. 8: Raise Δ T (upper graph) and drop - Δ T (lower graph) of egg temperature (C°) in small (filled circles) and big nests (open circles) during 20 minutes. Mean values of three smallest and biggest nests are given.

DISCUSSION

Although *Remiz pendulinus* is regarded as a sexually dimorphic species (SVENSSON 1984, GLUTZ et al. 1973), Franz (1988, 1991) stresses the difficulty for distinguishing between some males and females. In our populations, and with respect to the measured parameters, differences were only found for width of the mask and for weight (Tab. 3). However, the higher weight losses in polygynous males may be an indication of high investment in nest building which requires time and energy and may constrain other activities, like foraging.

Sexual dimorphism in polygynous species is mainly regarded as a result of intense intrasexual selection and predicts that mating success will increase with the intensity of conspicuous characteristics (HALLIDAY 1980). We therefore expect variation in the phenotypic attributes between unsuccessful, monogamous and polygynous males. FRANZ (1989, 1991) determined longer wing length for polygynous males. Our results, however, fail to establish any significant differences between these three male categories for wing length or for other morphological parameters which might be related to male quality (Tab. 3).

Calling near the unfinished nest is one of the most important features of a male penduline tit's courtship (FRANZ & THEISS 1983). We therefore expect differences in calling intensity between unmated, monogamous and polygynous males. Although song intensity, sometimes regarded as an indicator of a male's energetic condition (see REID 1987, REID et al. 1990), has been shown to affect mating success (ALATALO et al. 1990), we did not find such differences among the three male categories.

The lack of phenotypic variation and courtship intensity among males with different mating success suggests that females use other criteria for choosing a mate.

Several studies have indicated a strong correlation between habitat quality with reference to essential resources for reproductive success, female distribution and the formation of mating systems (VERNER & WILLSON 1966, 1969, ORIANS 1969, EMLEN & ORING 1977, ORING 1982).

For the penduline tit, food distribution has been shown to be abundant and hence facilitates uniparental care with high feeding frequency (VALERA 1988). We therefore conclude that habitat quality is not a significant cue used by females in mate choice. Our results indicate that varying male mating success does not correlate with habitat parameters for food resources (FRANZ & THEISS 1983, FRANZ et al. 1979) and nest material resources (LÖHRL 1981, VALERA 1988). Habitat quality may be partly influenced by the distribution of old nests, which are a source for nest material (FRANZ et al. 1979), and many males choose habitats containing old nests. The relative lack of importance of the nest site may be the consequence of low predation rates (FRANZ et al. 1979).

Our results support the importance of nest quality for female choice. As known for other species, like *Ploceus cucullatus* (COLLIAS & COLLIAS 1984), nest quality correlates with a male's experience and ability at nest building. In contrast to many other species, like bowerbirds, where females do not benefit from male performance (COLLIAS & COLLIAS 1984), our experiments suggests that female penduline tits benefit directly by choosing a high quality nest. Hence, female selection of the best nest available has important implications for the competitive behaviour between males, favouring those males which build better nests (COLLIAS & VICTORIA 1978).

Literature

ALATALO, R.V., LUNDBERG, A. & GLYNN, C. 1986: Female pied flycatcher choose territory quality and not male characteristics. Nature, London. 323: 152 - 153.

- -, GLYNN, C. & LUNDBERG, A. 1990: Singing rate and female attraction in the pied flycatcher: an experiment. Anim. Behav.39: 601 - 603.

ANDERSSON, M.B. 1982: Female choice selects for extreme tail lenght in a widowbird. Nature, London. 299: 818 - 820.

BORGIA, G. 1987: A critical review of sexual selection models, in: Sexual Selection: Testing the Alternative (J.W. Bradbury and M.B Andersson, eds.), pp. 55 - 66, Dahlem Konferenzen, Wiley, New York.

CATCHPOLE, C.K. 1980: Sexual selection and the evolution of complex songs among European warblers of the genus Acrocephalus. Behav. 74: 149 - 166.

COLLIAS, E. & COLLIAS, E.C. 1984: Nest building and bird behaviour. Princeton University Press, Princeton, N.J.

COLLIAS, N.E. & VICTORIA, J.K. 1978: Nest and mate selection in the village weaverbird *Ploceus cucullatus*. Anim. Behav. 26: 470 - 479.

EMLEN, S.T. & ORING, L.W. 1977: Ecology, sexual selection and the evolution of mating systems. Science 197: 215 - 223.

FRANZ, D. 1988: Paarungssystem der Beutelmeise (*Remiz pendulinus*) - ein Kampf der Geschlechter. J. Orn. 129: 107 - 111.

- - 1989: Paarungssystem und Fortpflanzungsstrategie der Beutelmeise *Remiz p. pendulinus* L. Diss. Uni. Erlangen-Nürnberg.

- - 1991: Paarungssystem und Fortpflanzungsstrategie der Beutelmeise *Remiz pendulinus*. J. Orn. 132: 241 - 266.

- -, KORTNER, W. & THEISS, N. 1979: Invasionsartiges Auftreten der Beutelmeise *Remiz pendulinus* im oberen Maintal 1978 und ihre Brutbiologie. Anz. orn. Ges. Bayern 18: 1 - 21.

- - & THEISS, N. 1983: Brutbiologie und Bestandsentwicklung einer farbberingten Population der Beutelmeise *Remiz pendulinus*. Verh. orn. Ges. Bayern 23: 393 - 442.

GLUTZ, V., BLOTZHEIM, U.N., BAUER, K.M. & BEZZEL, E. 1973: Handbuch der Vögel Mitteleuropas. Bd. 5. Akad. Verlags- gesellschaft, Frankfurt.

GREIG-SMITH, P.W. 1982: Seasonal patterns of song production by male stonechats (Saxicola torquata). Ornis. Scand. 13: 225 - 231.

HALLIDAY, T. 1980: Sexual Strategie. The University Press, Chicago 60637.

HEISLER, I.L. 1981: Offspring quality and the polygyny threshold: A new model for the "Sexy son hypothesis. Am. Nat. 117: 316 - 328.

HILL, G.E. 1990: Female house finches prefer colourful males: Sexual selection for a condition dependent trait. Anim. Behav. 40: 563 - 572.

KLEINBAUM, D.G. & KUPPER, L.L. 1978: Applied Regression Analysis and other Multivariable Methods. Duxbury Press, Boston, Massachusetts.

LENINGTON, S. 1980: Female choice and polygyny in red-winged blackbirds. Anim. Behav. 28: 347 - 361.

LÖHRL, H. 1981: Verhaltensmerkmale der Familie Remizidae (B). J. Orn. 122: 307 - 309.

ORIANS, G.H. 1969: On the evolution of mating systems in birds and mammals. Am. Nat. 103: 589 - 603.

ORING, L.W. 1982: Avian mating systems. In: D.S. FARNER, J.R. KING & K.C. PARKER (eds.): Avian Biology Vol. 6: 1 - 92. Academic Press, New York.

PERSSON, O. & ÖHRSTRÖM, P. 1985: Finns det nagra regler ipungmesens *Remiz pednulinus* parbildning? Var Fagelvärld 44: 135 - 144.

PRUM, R.O. 1985: The displays of the white-throated manakin *Corapipo gutturalis* in Suriname. Ibis 128: 91 - 102.

REID, M.L. 1987: Costliness and reability in the singing vigour of Ipswich sparrow. Anim. Behav. 35: 1735 - 1763.

- - & WEATHERHEAD, P.J. 1990: Mate choice criteria of Ipswich sparrows: the importance of variability. Anim. Behav. 40: 538 - 544.

SEARCY, W.A. 1988: Dual intersexual and intrasexual functions of song in red-winged blackbirds. Acta XIX Congr. Intern. Ornithol. Vol. I, 1373 - 1382.

SVENSSON, L. 1984: Identification Guide to European Passerines. 3. Aufl. Stockholm.

VALERA, F. 1988: Expansión y Biología de Reproducción de *Remiz pendulinus* en el Valle del Guadalquivir. D. Phil. Thesis, Univ. of Granada, Granada.

VAN RHIJN, J.G. 1991: The Ruff, Academic press inc. San Diego, CA 92101.

WHITE, F.N. & KINNEY, J.L. 1974: Avian incubation. Science 186: 107 - 115.

WITTENBERGER, J.F. 1979: The evolution of mating systems in birds and mammals. In: P. MARLER & J. VANDENBERGER (eds.): Handbook of Behavioural Neurobiology 3. Social Behaviour and Communication. Plenum Press, New York.

ZAR, J.H. 1989: Biostatistical analysis, 2nd ed. Englewood Cliffs, N.J.: Prentice-Hall 1984.

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