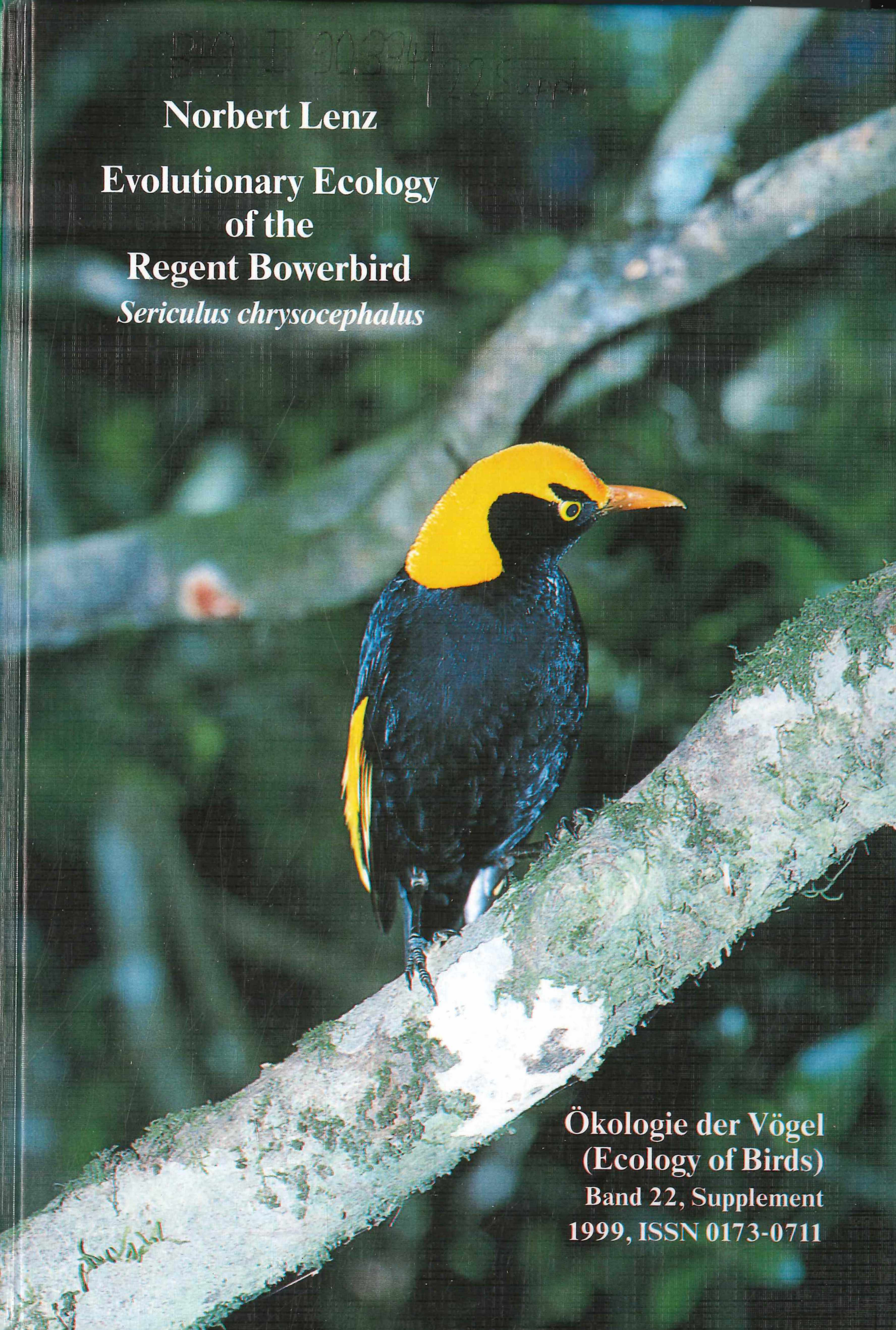

Norbert Lenz

Evolutionary Ecology of the Regent Bowerbird

Sericulus chrysocephalus

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Key words: Regent Bowerbird, *Sericulus chrysocephalus*, Ptilonorhynchidae, evolutionary ecology, sexual selection, mating systems, sexual dimorphism, frugivory, population parameters, operational sex ratio, display courts, site selection, female mate-choice decisions, male-male competition, emancipated males, uniparental brood care, polybrachygyny.

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Ludwigsburg
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Cover photograph: The Regent Bowerbird *Sericulus chrysocephalus* is an endemic species of the rainforests of central eastern Australia (photograph by Norbert Lenz).

Einbandfoto: Der Gelbnacken-Laubenvogel *Sericulus chrysocephalus* ist ein Endemit der Regenwälder des mittleren Ost-Australien (Fotografie von Norbert Lenz).

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Summary

Aspects of the evolutionary ecology of the Regent Bowerbird *Sericulus chrysocephalus* were studied in dry rainforest of the Sarabah Range in south-eastern Queensland from 1989 to 1992, supplemented by data collected in zoological collections between 1990 and 1998. This species differs from most other bowerbirds (Ptilonorhynchidae) in showing striking sexual plumage dimorphism and in building small and meagrely-decorated bowers, a combination of characteristics that has been attributed to an early stage in the evolution of bower building. The objectives of this study were to describe the mating system of the Regent Bowerbird, in particular bower building and associated behaviour, and to investigate life-history aspects that may have been important in the evolution of its mating system, in order to examine the position of the species in the evolution of the bowerbird family.

Variation in morphology and plumage was studied to allow determination of the age and sex of individuals. Males attain full adult plumage in their seventh year, considerably later than females, which do not change plumage colour after moulting into second-year plumage. Adult males have shorter wings and tails than immature males, possibly an adaptation to courtship displays in dense vegetation. Males are smaller than females, in accordance with congeners but in contrast with species in other bowerbird genera.

The diet of birds other than nestlings was mainly frugivorous, supplemented by invertebrates, nectar and leaves. A comparison with the diets of two sympatric species of the bowerbird family showed more dietary overlap with the non-monogamous, bower-building Satin Bowerbird *Ptilonorhynchus violaceus* than with the monogamous Green Catbird *Ailuroedus crassirostris*, which does not build bowers. However, all three species showed considerable dietary overlap. Unpredictability in fruit availability may have been a factor precluding non-monogamous bowerbirds from economically defending territories, but there was no simple dichotomy between diets of monogamous and non-monogamous species.

Regent Bowerbirds showed high survival rates. Mean annual survival rates were higher in males than in females, and, in both males and females, higher in older birds than in younger ones. Males which survived the relatively high juvenile mortality had an expectation of almost eight years of further life as adults. The high survival rates may have caused sexual selection through promoting age-related differences in male characteristics. Delayed maturity in males may have been a consequence of sexual selection, and resulted in a female-biased operational sex ratio of about two adult females per adult male.

Most adult males observed regularly were found to be maintaining bowers. Bowers were very difficult to find, due to their small size, inconspicuous decoration and concealed siting. On an average, bowers consisted of 432 sticks and contained 10.3 decoration objects. Bowers were widely spaced, with a mean nearest-neighbour distance of 195 m, and often located close to a ridgetop.

A discriminant function analysis revealed that males selected sites for bower building that were characterized by a large number of lianas, a high percentage of liana-thicket cover, a low percentage of open forest floor, a low canopy height, and a high percentage of open canopy. A second discriminant function analysis showed that bower sites of Regent Bowerbirds were characterized by higher percentages of liana-thicket cover, larger numbers of lianas, lower percentages of shrub- as well as herb- and grass-cover, and larger distances to the edge of the rainforest than those of sympatric Satin Bowerbirds. A total of 1516 hours of hide-based observations of bower activities revealed that bower-owning adult males spent only 3.2 % of daylight hours attending their bowers, whereas subadult males invested 11.8 % of daylight hours in bower attendance. Both figures are well below comparable figures for species in other bowerbird genera.

Males displayed at bowers and in trees, but copulation only took place after bower displays. Most courtship displays, including all displays that led to a copulation, were observed after a female had been escorted to a bower by its owner, indicating that, in contrast to other bowerbird species, the initial interaction between males and females took place in the canopy rather than at bowers. Females visited more than one bower within a mating season. The duration of their bower visits was correlated with a measure of bower quality but not with numbers of decorations. Successful courtship displays had a mean duration of 24.5 minutes and lasted several times longer than in other bowerbird species, suggesting that display performance may be of particular importance. Males destroyed bowers of other males, mostly their nearest neighbours, and stole decorations from them. The mean rates of bower destruction (0.246 per bower per day) and decoration stealing (0.156 per bower per day) were higher than in species with larger interbower distances. In contrast to other species, bower raiding frequently led to abandoning of bowers and changes of bower locations. Building a new bower may be profitable because Regent Bowerbird males cannot defend their bowers effectively in the small percentage of daytime they spend at them, whereas suitable bower sites may be common in their densely-vegetated habitat. Direct aggressive encounters of males were rare, but observations of agonistic interactions indicated that male dominance may be important for the ability to hold a bower.

Breeding biology and parental behaviour resembled other bowerbird species with emancipated males and uniparental female brood care. Egg-laying was sufficiently asynchronous (c. three months) to provide multiple mating opportunities for individual males. The predominance of insects in the nestling diet may have facilitated uniparental care.

The mating system of the Regent Bowerbird can be described as 'dispersed male-dominance polybrachygyny'. Similarities and differences to other bowerbird species as well as factors that may have been important in the evolution of the family are discussed. The same forces of sexual selection may have been important in all bower-building species, shaping similar patterns of female mate-choice decisions and male-male competition. The interspecific differences in elaborateness of male plumages and bowers, however, appear to be influenced strongly by habitat differences and associated differences in plumage conspicuousness and predation, population density and bower-site availability, suggesting that the pressures of natural selection should not be ignored.

Zusammenfassung

Aspekte der Evolutionsökologie des Gelbnacken-Laubenvogels oder Samtgoldvogels *Sericulus chrysocephalus* wurden von 1989 bis 1992 in einem Trockenregenwald der Sarabah-Bergkette in Südost-Queensland untersucht, ergänzt durch Daten, die zwischen 1990 und 1998 in zoologischen Sammlungen erhoben wurden. Diese Art unterscheidet sich von den meisten anderen Laubenvögeln (Ptilonorhynchidae) durch auffälligen Sexualdimorphismus im Gefieder und durch kleine, spärlich dekorierte Lauben, eine Merkmalskombination, die einem frühen Stadium in der Evolution des Laubenbaus zugeschrieben worden ist. Ziele der vorliegenden Arbeit waren die Beschreibung des Partnerschaftssystems des Gelbnacken-Laubenvogels, insbesondere Laubenbau und damit verbundene Verhaltensweisen, sowie die Untersuchung von Aspekten seiner Biologie, die bei der Evolution seines Partnerschaftssystems von Bedeutung gewesen sein könnten, damit die Stellung der Art in der Evolution der Familie der Laubenvögel untersucht werden kann.

Die Variabilität von Morphologie und Gefieder wurde untersucht, um die Alters- und Geschlechtsbestimmung von Individuen zu ermöglichen. Männchen erreichen das vollständige Adultkleid in ihrem siebten Lebensjahr, beträchtlich später als Weibchen, deren Gefiederfärbung sich nach der Mauser in das zweite Sommerkleid nicht mehr verändert. Adulte Männchen haben kürzere Flügel- und Schwanzfedern als immature Männchen, möglicherweise eine Anpassung an Balz in dichter Vegetation. In Übereinstimmung mit gattungsgleichen Arten, aber im Gegensatz zu den Arten anderer Laubenvogelgattungen, sind Männchen kleiner als Weibchen.

Außer bei den Nestlingen bestand die Nahrung hauptsächlich aus Früchten, ergänzt durch Invertebraten, Nektar und Blätter. Ein Vergleich mit der Nahrung von zwei sympatrischen Arten der Familie der Laubenvögel zeigte mehr Nischenüberlappung mit dem nichtmonogamen, Lauben bauenden Seidenlaubenvogel *Ptilonorhynchus violaceus* als mit dem monogamen Grünkatzenvogel *Ailuroedus crassirostris*, der keine Lauben baut. Alle drei Arten zeigten jedoch große Nischenüberlappung in ihrer Nahrungswahl. Unberechenbarkeit in der Verfügbarkeit von Früchten könnte ein Faktor gewesen sein, der nichtmonogame Laubenvögel daran gehindert hat, Reviere ökonomisch zu verteidigen; es ließ sich aber keine einfache Trennung zwischen den Nahrungsspektren monogamer und nichtmonogamer Arten feststellen.

Gelbnacken-Laubenvögel wiesen hohe Überlebensraten auf. Die mittleren jährlichen Überlebensraten waren bei Männchen höher als bei Weibchen und - sowohl bei Männchen als auch bei Weibchen - bei älteren Vögeln höher als bei jüngeren. Männchen, die die relativ hohe Jugendsterblichkeit überlebten, hatten eine Lebenserwartung von fast acht Jahren weiteren Lebens als adultes Individuum. Die hohen Überlebensraten könnten sexuelle Selektion durch die Förderung von Unterschieden in Merkmalen der Männchen verursacht haben. Das spätere Erreichen des Adultstadiums bei Männchen könnte eine Folge von sexueller Selektion gewesen sein und führte zu einem zugunsten der Weibchen verschobenen effektiven Geschlechterverhältnis von etwa zwei adulten Weibchen pro adultem Männchen.

Von den adulten Männchen, die regelmäßig beobachtet wurden, unterhielten die meisten Lauben. Aufgrund ihrer geringen Größe, der unauffälligen Dekoration und der verborgenen Lage war es sehr schwierig, die Lauben zu finden. Die Lauben bestanden im Durchschnitt aus 432 Stöckchen und enthielten durchschnittlich 10,3 Dekorationsobjekte. Die Lauben waren in Abständen verteilt, mit einer mittleren Distanz von 195 m zum nächsten Nachbarn, und befanden sich häufig im oberen Bereich eines Bergrückens.

Eine Diskriminanzanalyse ergab, dass Männchen zum Laubenbau Plätze wählten, für die eine große Anzahl von Lianen, ein hoher Anteil von Lianendickicht, ein geringer Anteil von offenem Waldboden, eine geringe Kronendachhöhe und ein hoher Anteil von offenem Kronendach charakteristisch waren. Eine zweite Diskriminanzanalyse zeigte, dass Laubenplätze von Gelbnacken-Laubenvögeln im Vergleich zu denen sympatrischer Seidenlaubenvögel durch höhere Anteile von Lianendickicht, größere Anzahlen von Lianen, geringere Anteile von Strauch- sowie Kraut- und Grasdeckung und durch größere Entfernungen zum Regenwaldrand gekennzeichnet waren.

Insgesamt 1516 Stunden von Tarnzelten aus durchgeführte Beobachtungen der Aktivitäten an Lauben ergaben, dass sich Lauben besitzende adulte Gelbnacken-Laubenvogel-Männchen nur 3,2 % der Tageslicht-Stunden bei ihren Lauben aufhielten, subadulte Männchen hingegen 11,8 % der Tageslicht-Stunden. Beide Werte liegen deutlich unter vergleichbaren Angaben für Arten anderer Laubenvogelgattungen.

Die Männchen balzten an Lauben und in Bäumen, Kopulationen fanden aber nur nach Balz an Lauben statt. Die meisten Balzfolgen, darunter alle Balzfolgen, die zu einer Kopulation führten, wurden beobachtet, nachdem ein Weibchen von einem Laubeninhaber zu seiner Laube geleitet worden war; dieser Ablauf deutet darauf hin, dass - im Gegensatz zu anderen Laubenvogelarten - der erste Kontakt zwischen Männchen und Weibchen im Kronendach stattfand und nicht an den Lauben. Weibchen besuchten mehr als eine Laube im Laufe einer Paarungssaison. Die Dauer ihrer Laubenbesuche korrelierte mit einem Index der Laubenqualität, jedoch nicht mit der Anzahl von Dekorationsobjekten. Erfolgreiche Balzfolgen dauerten im Mittel 24,5 Minuten und waren um ein mehrfaches länger als bei anderen Laubenvogelarten, was nahelegt, dass die Balzleistung von besonderer Bedeutung ist.

Männchen zerstörten die Lauben anderer Männchen, meistens die ihrer nächsten Nachbarn, und stahlen Dekorationsobjekte von ihnen. Die durchschnittliche Häufigkeit von Laubenzerstörung (0,246-mal pro Laube und Tag) und Stehlen von Dekorationen (0,156-mal pro Laube und Tag) war größer als bei Arten mit größeren Entfernungen zwischen den Lauben. Im Gegensatz zu anderen Arten führten Laubenüberfälle häufig zum Aufgeben von Lauben und zum Verlagern von Laubenplätzen. Der Bau einer neuen Laube könnte profitabel sein, da die Gelbnacken-Laubenvogel-Männchen in dem geringen Teil der Tageszeit, den sie an ihren Lauben verbringen, diese nicht wirkungsvoll verteidigen können, wohingegen zum Laubenbau geeignete Plätze im dicht bewachsenen Lebensraum häufig sein könnten. Direkte aggressive Auseinandersetzungen zwischen

Männchen waren selten, doch deuteten Beobachtungen von agonistischen Interaktionen darauf hin, dass die Dominanz von Männchen für die Fähigkeit, eine Laube zu halten, von Bedeutung ist.

Brutbiologie und Brutpflege ähnelten anderen Laubenvogelarten, deren Männchen sich nicht am Brutgeschäft beteiligen. Die Eiablage der Weibchen einer Population war asynchron genug (ca. drei Monate), um einzelnen Männchen Kopulationen mit mehreren Weibchen zu ermöglichen. Das Überwiegen von Insekten in der Nestlingsnahrung könnte die ausschließliche Brutpflege durch Weibchen erleichtert haben.

Das Partnerschaftssystem des Gelbnacken-Laubenvogels kann als Polybrachygynie verteilter, dominanter Männchen bezeichnet werden. Ähnlichkeiten mit bzw. Unterschiede zu anderen Laubenvogelarten sowie Faktoren, die in der Evolution der Familie wichtig gewesen sein könnten, werden diskutiert. Die gleichen Einflüsse sexueller Selektion könnten bei allen Lauben bauenden Arten von Bedeutung gewesen sein und ähnliche Muster bei der Wahl der Paarungspartner durch Weibchen und der Konkurrenz unter Männchen geformt haben. Die interspezifischen Unterschiede in der Prächtigkeit der Männchengefieder und der Lauben scheinen jedoch stark durch Habitatunterschiede und damit verbundene Differenzen bei Gefiederauffälligkeit und Episitismus, Populationsdichte und Verfügbarkeit von Laubenplätzen beeinflusst zu sein, was nahe legt, dass die Selektionsdrucke der natürlichen Auslese nicht ignoriert werden sollten.

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1 Introduction

1.1 Sexual selection and the evolution of mating systems

CHARLES DARWIN's most important contributions to evolutionary theory were the concepts of natural selection (DARWIN 1859) and sexual selection (DARWIN 1871). Natural selection theory is concerned with the evolution of characters involved in natural competition, whereas sexual selection theory is concerned with the evolution of characters solely involved in the competition for mates.

Two modes of sexual selection have been proposed: intrasexual selection and intersexual selection (DARWIN 1871; MAYNARD SMITH 1978, 1987; BRADBURY & DAVIES 1987; HARVEY & BRADBURY 1991; ANDERSSON 1994; JOHNSGARD 1994; MØLLER 1994; COCKBURN 1995). Intrasexual selection involves the direct competition for mates between members of the same sex, usually competition among males for females. Intersexual selection involves the active choice by one sex of particular individuals of the other, usually the choice of males by females.

The concept of sexual selection originated, and is still best known, as an attempt to explain the evolution of exaggerated male characters such as the plumages of birds of paradise and the horns of antelopes, which appear to be disadvantageous in terms of natural selection but which are important to sexual reproduction (DARWIN 1871; KREBS & DAVIES 1987; HARVEY & BRADBURY 1991; ANDERSSON 1994). However, DARWIN (1871) conceded that it is often impossible to distinguish between the effects of natural and sexual selection, as the latter is a component of the former.

While DARWIN's concept of natural selection had an immediate impact on biological theory (MAYR 1982), it is only since the 1960s that sexual selection has received wide recognition and has become an important topic in evolutionary biology (ANDERSSON & BRADBURY 1987; HARVEY & BRADBURY 1991; ANDERSSON 1994; MØLLER 1994). Acceptance of the sexual selection concept has been furthered by numerous field studies of animal behaviour, during which more and more examples of traits not easily explained by natural selection were studied (ANDERSSON & BRADBURY 1987; ANDERSSON 1994).

The fundamental unit of selection is the individual organism (DARWIN 1859, 1871; MAYR 1982), and the mating system of a species or a population is the outcome of the behaviour of individuals competing to maximize their reproductive success (TRIVERS 1972; EMLEN & ORING 1977; DAVIES 1991). Comparative field studies of behavioural and ecological traits of closely-related species have revealed the importance of certain environmental factors in the evolution of mating systems (see references in EMLEN & ORING 1977; WITTENBERGER 1979; ORING 1982).

EMLEN & ORING (1977) synthesized natural history data into a theory of mating system evolution. They hypothesized that the spatial and temporal distribution of critical resources and of sexually receptive mates determine the potential for individuals to defend and to monopolize resources and/or mates. According to Emlen & Oring (l.c.), the prerequisite for the evolution of a monogamous mating system is the economic defendability of a mate, and the prerequisite for a polygamous mating system is the capacity to economically monopolize several mates. The sex with multiple mating opportunities is much more often the male (polygynous mating systems) than the female (polyandrous mating systems).

Most species of mammals are polygamous, whereas more than 90 per cent of bird species are categorized as monogamous (Lack 1968; Orians 1969; Wittenberger 1979; Oring 1982; Brooke & Birkhead 1991; de Juana 1992). The laying of eggs, in conjunction with homoiothermy, requires considerable parental care and investment for successful rearing of young, which has prevented the evolution of non-monogamous mating systems in most avian species (Trivers 1972; Oring 1982; Bezzel & Prinzinger 1990; de Juana 1992).

Therefore, the small but taxonomically diverse array of bird species where non-monogamous mating systems have evolved is of particular interest to evolutionary biologists. Among the taxa most important in the study of sexual selection and mating system evolution are species of grouse (Tetraonidae), cotingas (Cotingidae), manakins (Pipridae), lyrebirds (Menuridae), birds of paradise (Paradisaeidae), and bowerbirds (Ptilonorhynchidae).

1.2 The family of bowerbirds

The passerine bird family of bowerbirds is endemic to the Australo-Papuan region (Keast 1961, 1981; Sibley & Ahlquist 1985). The bowerbird family contains eight genera comprising c. 18 to 20 species (Wolters 1975-1982; Howard & Moore 1980; Walters 1980; Beehler & Finch 1985; Sibley & Monroe 1990; Christidis & Boles 1994).

The name bowerbird is used for both the entire family and as part of the English name for most species (see Table 1.1) with the exception of the three species of the genus *Ailuroedus*, the so-called catbirds (see Plate 1). The name bowerbird refers to the decorated terrestrial display courts or bowers, which the males of all bowerbird genera except *Ailuroedus* build. In this paper the term 'bowerbird' is used only for those members of the family that build display courts. When referring to the entire family the term 'bowerbird family' is used.

The preparation of specific display courts which males use during their sexual displays is not restricted to bowerbirds, but it reaches its most complex and elaborate level in the whole animal kingdom in this family (Gilliard 1963, 1969; Borgia et al. 1985; Diamond 1986a,b). Four basic types of courts or bowers have been recognized, though bower structure and the types of decoration objects used vary between and within species (Marshall 1954, 1956; Gilliard 1956, 1969; Cooper & Forshaw 1977; Borgia et al. 1985; Diamond 1987; Pruett-Jones & Pruett-Jones 1994; Frith & Frith 1998a):

Table 1.1. Species of bowerbirds (Ptilonorhynchidae), their bower types and a selection of recent studies on various aspects of their biology.
Tab. 1.1. Laubenvogelarten (Ptilonorhynchidae), ihre Laubenbauweise und eine Auswahl neuerer Untersuchungen verschiedener Aspekte ihrer Biologie.

English name Englischer Name	German name Deutscher Name	Scientific name Wissenschaftl. Name
White-eared Catbird	Weißohr-Katzenvogel	*Ailuroedus buccoides*
Spotted Catbird	Schwarzohr-Katzenvogel	*Ailuroedus melanotis*
Green Catbird	Grünkatzenvogel	*Ailuroedus crassirostris*
Tooth-billed Bowerbird	Zahnlaubenvogel	*Scenopoeetes dentirostris*
Archbold's Bowerbird	Archboldlaubenvogel	*Archboldia papuensis*
Golden-fronted Bowerbird	Gelbscheitelgärtner	*Amblyornis flavifrons*
Macgregor's Bowerbird	Goldhaubengärtner	*Amblyornis macgregoriae*
Streaked Bowerbird	Rothaubengärtner	*Amblyornis subalaris*
Vogelkop Bowerbird	Hüttengärtner	*Amblyornis inornatus*
Golden Bowerbird	Säulengärtner	*Prionodura newtoniana*
Flame Bowerbird	Goldlaubenvogel	*Sericulus aureus*
Fire-maned Bowerbird	Rotscheitel-Laubenvogel	*Sericulus bakeri*
Regent Bowerbird	Gelbnacken-Laubenvogel	*Sericulus chrysocephalus*
Satin Bowerbird	Seidenlaubenvogel	*Ptilonorhynchus violaceus*
Western Bowerbird	Westl. Fleckenlaubenvogel	*Chlamydera guttata*
Spotted Bowerbird	Östl. Fleckenlaubenvogel	*Chlamydera maculata*
Great Bowerbird	Graulaubenvogel	*Chlamydera nuchalis*
Yellow-breasted Bowerbird	Dreigang-Laubenvogel	*Chlamydera lauterbachi*
Fawn-breasted Bowerbird	Braunbauch-Laubenvogel	*Chlamydera cerviniventris*

(1) *Court*: Males of the Tooth-billed Bowerbird *Scenopoeetes dentirostris* do not build a bower, but clear leaf litter from an area of forest floor, typically encompassing the trunk base of a tree, and decorate it with selected leaves laid paler side uppermost (see Plate 2).
(2) *Mat bower*: Males of Archbold's Bowerbird *Archboldia papuensis* accumulate and decorate a thick mat of fern fronds and drape perches above it with stems of epiphytic orchids (see Plates 3-4).
(3) *Maypole bower*: Males of the four species of *Amblyornis* and of the monotypic Golden Bowerbird *Prionodura newtoniana* accumulate an abundance of sticks horizontally around a central pole, a sapling or a treefern (see Fig. 1.1 and Plate 5). Two species build a hut-like structure around this maypole. The display site is a cleared and decorated court surrounding the maypole, or a display perch integrated into the bower.

Bower type Laubenbauweise	Recent studies Neuere Untersuchungen
None/Keine	None/Keine
None/Keine	FRITH 1994
None/Keine	DONAGHEY 1981; INNIS & MCEVOY 1992
Court/Tenne	FRITH & FRITH 1985b, 1993, 1994b, 1995; FRITH et al. 1994; FRITH & MCGUIRE 1996
Mat/Matte	FRITH & FRITH 1988, 1990b, 1994a; FRITH et al. 1996
Maypole/Maibaum	DIAMOND 1982a
Maypole/Maibaum	PRUETT-JONES & PRUETT-JONES 1982, 1983, 1985
Maypole/Maibaum	None/Keine
Maypole/Maibaum	DIAMOND 1986a, 1987, 1988
Maypole/Maibaum	FRITH 1989; FRITH & FRITH 1998b
Avenue/Allee	BELL 1970
Avenue/Allee	MACKAY 1989
Avenue/Allee	DISNEY & LANE 1971; BARDEN 1977; LENZ 1994
Avenue/Allee	VELLENGA 1970, 1980a,b; DONAGHEY 1981; BORGIA 1985a,b, 1986a,b, 1993; BORGIA & GORE 1986; LOFFREDO & BORGIA 1986; BORGIA et al. 1987; BORGIA & COLLIS 1989, 1990; COLLIS & BORGIA 1992, 1993
Avenue/Allee	BRADLEY 1987
Avenue/Allee	FRITH & FRITH 1990c; BORGIA & MUELLER 1992; BORGIA 1995a,b; FRITH et al. 1995
Avenue/Allee	VESELOVSKÝ 1978, 1979; FRITH & FRITH 1990a; FRITH et al. 1994, 1995; BORGIA 1995a
Avenue/Allee	GILLIARD 1969; FRITH & FRITH 1989
Avenue/Allee	PECKOVER 1970; FRITH & FRITH 1989

(4) *Avenue bower*: Males of the species in the genera *Sericulus*, *Ptilonorhynchus* and *Chlamydera* build parallel walls of sticks or stems of grass, inserted vertically into a horizontal platform made from the same material (see Fig. 1.2 and Plate 6). The walls enclose the bower avenue. Parts of the inside walls are painted by the males through the application of masticated vegetable matter onto them. Either the avenue or the immediate bower surroundings or both are decorated.

Bowers have attracted much attention since their discovery in the nineteenth century (e.g. GOULD 1848, 1865; NUBLING 1921, 1939; STRESEMANN 1953; MARSHALL 1954). But only in recent years have intensive long-term field studies of bowerbird behaviour and ecology been undertaken, stimulated by the debate over sexual selection and the evolution of mating systems (BORGIA et al. 1985; BORGIA 1986a; PRUETT-JONES & PRUETT-JONES 1994).

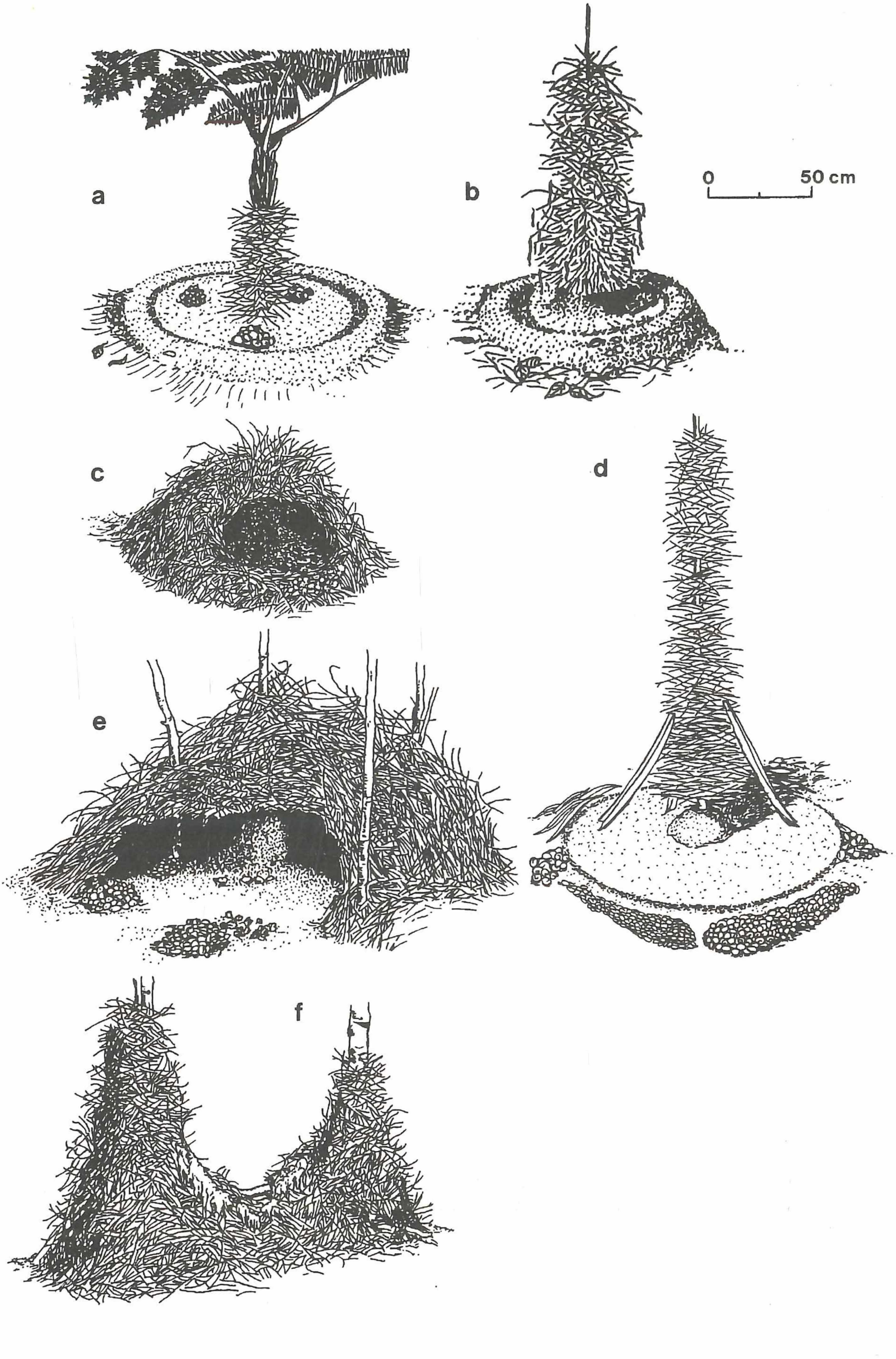
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Figure 1.1 (on page 18). Maypole bowers (drawn to scale after GILLIARD 1969; COOPER & FORSHAW 1977; DIAMOND 1982a, 1987; COATES 1990): (a) Golden-fronted Bowerbird *Amblyornis flavifrons*; (b) Macgregor's Bowerbird *A. macgregoriae*; (c) Streaked Bowerbird *A. subalaris*; (d) Vogelkop Bowerbird *A. inornatus*, Kumawa population; (e) Vogelkop Bowerbird *A. inornatus*, Tamrau-Wandammen populations; (f) Golden Bowerbird *Prionodura newtoniana*.
Abb. 1.1 (auf Seite 18). Maibaumlauben (maßstabsgetreu gezeichnet nach GILLIARD 1969; COOPER & FORSHAW 1977; DIAMOND 1982a, 1987; COATES 1990): (a) Gelbscheitelgärtner *Amblyornis flavifrons*; (b) Goldhaubengärtner *A. macgregoriae*; (c) Rothaubengärtner *A. subalaris*; (d) Hüttengärtner *A. inornatus*, Kumawa-Population; (e) Hüttengärtner *A. inornatus*, Tamrau-Wandammen-Populationen; (f) Säulengärtner *Prionodura newtoniana*.

The only species in the bowerbird family in which a monogamous mating system is found are those that do not build a display court: the catbirds (DONAGHEY 1981; FRITH & FRITH 1985b; COATES 1990). All bower-building species are assumed to be non-monogamous (the classification of their mating systems is discussed in Chapter 9), though conclusive observational evidence of multiple matings of single males has been produced for only some of them (BORGIA 1985a, 1995b; BORGIA et al. 1985; DONAGHEY et al. 1985; DIAMOND 1986b; FRITH et al. 1996).

Best understood is the reproductive biology and evolutionary ecology of the Satin Bowerbird *Ptilonorhynchus violaceus*, a species that has been studied intensively since the 1960s (see selection of references in Table 1.1). The Satin Bowerbird is sexually dimorphic in plumage (see Plates 7-8), adult males being glossy blue-black and females dull green-brown; males attain adult plumage considerably later than females (VELLENGA 1980a). Immature and adult males build and decorate avenue bowers (see Plates 9-10), but bowers of younger males are more rudimentary (VELLENGA 1970, 1980b, 1986). Males maintain a strong fidelity to their bower sites, which are often used by the same individual over several years (VELLENGA 1980b; DONAGHEY 1981). Males frequently visit and damage bowers of other males, pulling out sticks and stealing decoration objects (VELLENGA 1970; DONAGHEY 1981). During the mating season males perform arboreal and bower displays, but mating always takes place at or near the bower (VELLENGA 1970; DONAGHEY 1981). Brood care is performed solely by the female (PRATT 1974; VELLENGA 1980b; DONAGHEY 1981).

Questions concerning sexual selection in the Satin Bowerbird have been studied by BORGIA and co-workers in the 1980s, through simultaneously monitoring the bowers of more than twenty males of a population over several mating seasons (BORGIA 1985a, 1986a). Among the males studied, the distribution of copulations showed a strong skew, a small number of males accounting for the vast majority of matings (BORGIA 1985a). Females visited the bowers of several males before mating (BORGIA et al. 1985). The number of copulations of a male was significantly correlated with measures of bower quality and with the numbers of certain, locally rare, decoration types (BORGIA 1985a). Male mating success was inversely correlated with the frequency at which a male's

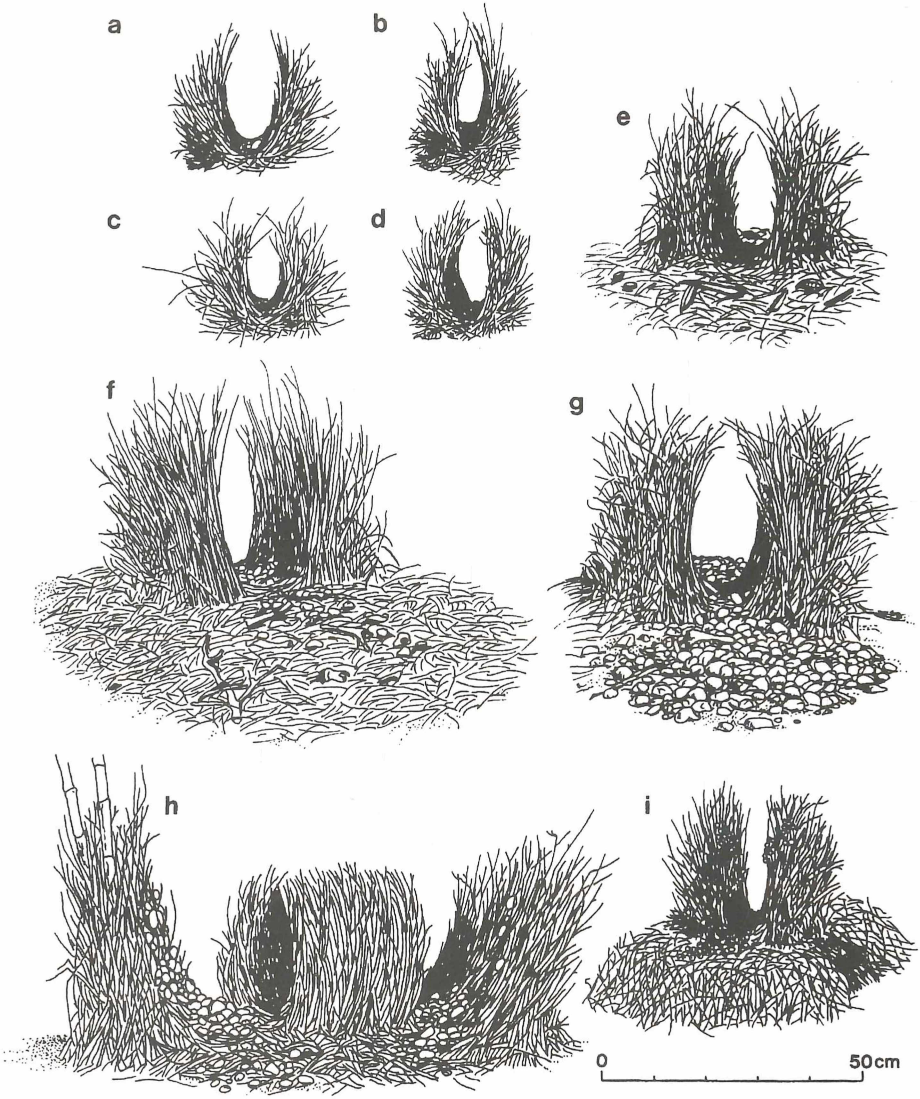


Figure 1.2. Avenue bowers (drawn to scale after GILLIARD 1969; COOPER & FORSHAW 1977; COATES 1990): (a) Flame Bowerbird *Sericulus aureus*, northern taxon *aureus*; (b) Flame Bowerbird *S. aureus*, southern taxon *ardens*; (c) Fire-maned Bowerbird *S. bakeri*; (d) Regent Bowerbird *S. chrysocephalus*; (e) Satin Bowerbird *Ptilonorhynchus violaceus*; (f) Spotted Bowerbird *Chlamydera maculata*; (g) Great Bowerbird *C. nuchalis*; (h) Yellow-breasted Bowerbird *C. lauterbachi*; (i) Fawn-breasted Bowerbird *C. cerviniventris*.

Abb. 1.2 (auf Seite 20). Alleelauben (maßstabsgetreu gezeichnet nach GILLIARD 1969; COOPER & FORSHAW 1977; COATES 1990): (a) Goldlaubenvogel *Sericulus aureus*, nördliches Taxon *aureus*; (b) Goldlaubenvogel *S. aureus*, südliches Taxon *ardens*; (c) Rotscheitel-Laubenvogel *S. bakeri*; (d) Gelbnacken-Laubenvogel *S. chrysocephalus*; (e) Seidenlaubenvogel *Ptilonorhynchus violaceus*; (f) Östlicher Fleckenlaubenvogel *Chlamydera maculata*; (g) Graulaubenvogel *C. nuchalis*; (h) Dreigang-Laubenvogel *C. lauterbachi*; (i) Braunbauch-Laubenvogel *C. cerviniventris*.

bower was destroyed and with the rate at which decoration objects were stolen from it (BORGIA 1985a). Bower quality was inversely correlated with "the number of destructions at bowers and the amount of destruction of bowers" (BORGIA 1985b, p. 91). Blue feathers were the most preferred of all decoration objects stolen from bowers, and the rate of stealing by males was significantly correlated with the number of feathers on their bowers (BORGIA & GORE 1986).

These results suggest that bowers and decoration objects are key elements of the sexual display of male Satin Bowerbirds and are important in influencing mate choice by females and male mating success. PRUETT-JONES & PRUETT-JONES (1983) and BORGIA et al. (1985) proposed the hypothesis that bower-building behaviour evolved as part of a mechanism allowing females to assess the quality of males as mates. The bower and its decoration objects represent an indicator or 'marker' of the resident male's status, on which female mate-choice decisions are based (the 'marker hypothesis'; PRUETT-JONES & PRUETT-JONES 1983; BORGIA et al. 1985).

To test the validity of this hypothesis as a general explanation for the evolution of bower building, knowledge of the evolutionary ecology of other bowerbird species is required. BORGIA (1985a, p. 269) suggested "that the ultimate basis for female choice may be the same" in all bower-building species, but females of different species may differ "in how they assess male quality".

Some bowerbirds are sexually dimorphic in plumage, some only slightly dimorphic and some monomorphic, and the degree of complexity of their bowers varies considerably (MARSHALL 1954; COOPER & FORSHAW 1977; DONAGHEY et al. 1985; COATES 1990; FRITH & FRITH 1998a). A comparison of the elaborateness of male plumages in bowerbirds with the elaborateness of their bowers led GILLIARD (1956, 1963, 1969) to suggest a 'transferral effect': the degree of ornamentation of the bower and that of the bird are inversely correlated, bowers and bower decorations have become secondary sexual characteristics, and decoration objects are a substitute for elaborate male plumage.

For example, in the species of the maypole-building genus *Amblyornis*, adult males of the Golden-fronted Bowerbird *A. flavifrons* and of Macgregor's Bowerbird *A. macgregoriae* are both elaborately ornamented with a large crest, yet build simple maypoles (see Fig. 1.1) with relatively few decorations (DIAMOND 1982a,b; PRUETT-JONES & PRUETT-JONES 1983). In contrast, the unornamented males of the Vogelkop Bowerbird *A. inornatus* build the most elaborate display structures of any animal species (DIAMOND 1986a, 1987). Males of the Streaked Bowerbird *A. subalaris* are intermediate, with shorter crests than those of male Golden-fronted and Macgregor's Bowerbirds and somewhat less ornamented bowers than those of the Vogelkop Bowerbird (DIAMOND 1982a). The position of the fifth maypole-building species, the Golden Bowerbird, is more difficult to categorize but is similar to the intermediate position of the Streaked Bowerbird (DIAMOND 1982a).

Within the group of species building avenue bowers, the brightly-coloured males of the *Sericulus* species build the smallest and least-decorated bowers (see Fig. 1.2a-d and Plates 11-12), whereas the rather dull males of the *Chlamydera* species build the largest avenue bowers (see Fig. 1.2f-i and Plates 13-16), with enormous numbers of decoration objects (COOPER & FORSHAW 1977; VESELOVSKÝ 1979; BORGIA 1995a). The Satin Bowerbird, the sole species in the genus *Ptilonorhynchus*, has an intermediate position (GILLIARD 1969; SCHODDE 1976).

If GILLIARD's hypothesis of the 'transferral effect' is correct, the genus *Sericulus* represents an early stage in the transfer of secondary sexual characteristics from elaborate male plumages to elaborate bowers. Therefore, the genus *Sericulus* would represent an early stage in the evolution of bower building, and knowledge of the biology and ecology of this genus would be of particular importance for an understanding of bowerbird evolution.

1.3 Questions concerning the Regent Bowerbird

In recent years intensive field studies on representatives of most bowerbird genera have been undertaken (see references in Table 1.1). The genus *Sericulus*, however, has only been the subject of a few short publications, mainly descriptions of single bowers (BELL 1970; BARDEN 1977; MACKAY 1989). As a result, it has largely been omitted from reviews about bowerbirds and the evolution of bower building (BORGIA et al. 1985; DIAMOND 1986b; BACKUS 1987; MÜLLER 1990; JOHNSGARD 1994; PRUETT-JONES & PRUETT-JONES 1994; FRITH & FRITH 1998a).

The only Australian representative of the genus *Sericulus* is the Regent Bowerbird *S. chrysocephalus*. Although it has been observed more often than its congeners from New Guinea, the Flame Bowerbird *S. aureus* and the Fire-maned Bowerbird *S. bakeri*, difficulties in observing the species in the wild have prevented field studies (BARDEN 1977), and most details of its biology remained unknown (DISNEY & LANE 1971; BORGIA et al. 1985).

Regent Bowerbirds have been studied in captivity by PHILLIPPS (1901-1911). His publications have often been quoted in the literature (e.g. MARSHALL 1954; ARMSTRONG 1965; GILLIARD 1969), but they are almost useless scientifically as PHILLIPPS frequently confused females and immature males, and his anthropomorphic jargon makes it very difficult to interpret his observations.

Due to the lack of field data, the biology of the Regent Bowerbird has been the subject of much speculation. In particular, it has been debated where and to what extent the species builds bowers (GILLIARD 1969; BORGIA et al. 1985). Only few bowers of the Regent Bowerbird have been found in the wild (BARDEN 1977), and it has been proposed that the species does not build them regularly (IREDALE 1950; GILLIARD 1969; DIAMOND 1982b) or uses them for a short time only (BELL 1970). It has also been claimed that Regent Bowerbird bowers may be attended by several males (SCHODDE & TIDEMANN 1990; LINDSEY 1992).

If any of these assertions were correct the Regent Bowerbird would contrast sharply with other bowerbird species, where males build bowers regularly, show a strong fidelity to bower sites and each bower is maintained by a single resident male (DONAGHEY 1981; PRUETT-JONES & PRUETT-JONES 1982; DIAMOND 1987; FRITH 1989; BORGIA 1993; FRITH & FRITH 1995, 1998a). Possible differences in bower function between the Regent Bowerbird and other bowerbird species could be related to differences in their respective stage in the transfer of secondary sexual characteristics from plumage to bower. However, a comprehensive study is required to compare the Regent Bowerbird with other bower-building species.

The present study shall fill this gap. It is mainly based on three years of field work on a Regent Bowerbird population in south-eastern Queensland. Whereas BORGIA (1985a,b, 1986a,b, 1993) could base his work on the Satin Bowerbird on previous studies by VELLENGA (1970, 1980a,b) and DONAGHEY (1981), such a background was largely missing for this work. Therefore, it was necessary to study aspects of the basic life history of the Regent Bowerbird in addition to its bower-building behaviour, in order to identify factors that may have been important in the evolution of its mating system. The main objectives of this study are:

- to analyse sex-related, age-related and geographical variation in morphology and plumage (Chapter 3);
- to document the foods and foraging of the species (Chapter 4);
- to investigate population parameters and their implications for the reproductive biology (Chapter 5);
- to describe the construction and decoration of Regent Bowerbird bowers, and to analyse bower site selection and spatial distribution (Chapter 6);
- to describe and analyse the behaviour of Regent Bowerbirds at their bowers, the sexual display, patterns of female visits and male interactions (Chapter 7; parts of this chapter have been published previously, see LENZ 1994);
- and to describe the breeding biology and parental behaviour (Chapter 8).

The information in this study shall make it possible to understand the mating system of the Regent Bowerbird, to make detailed comparisons with other bowerbird species, and to discuss the position of the Regent Bowerbird in the evolution of the bowerbird family.

2 Study Area and Methods

2.1 Study area

The study was conducted on a predominantly rainforest-covered mountain ridge in the central section of the Sarabah Range (28°10'00"S, 153°07'30"E) in south-eastern Queensland, central eastern Australia, 80 km to the south of Brisbane (as the bowerbird flies). This mountain ridge is situated between two creeks, Cainbable Creek in the west and Canungra Creek in the east, both tributaries of the Albert River. Elevation is mostly between 600 and 720 metres above sea level.

The study area is private property. Lamington National Park (20500 ha area, founded in 1915, as a part of the 'Central Eastern Australian Rainforest Reserves' on the World Heritage List) is bordering in the east, and Sarabah State Forest (State Forest 536, incorporated into Lamington National Park in 1990) in the north-west. The boundary of the study area was marked by the ecotone between rainforest (closed forest) and eucalypt forest (open forest) in the west, by the steep slope down to Canungra Creek in the east, and by clearings in the north and south (see Figs 2.1-2.2). These boundaries gave the study area a somewhat triangular shape, covering a rainforest area of 186.3 ha. Lamington National Park Road, mostly following the top of the ridge, divided the study area into a western and an eastern part. Several old timber-getters' tracks remained discernible in the area and could be used as an aid for orientation during field work.

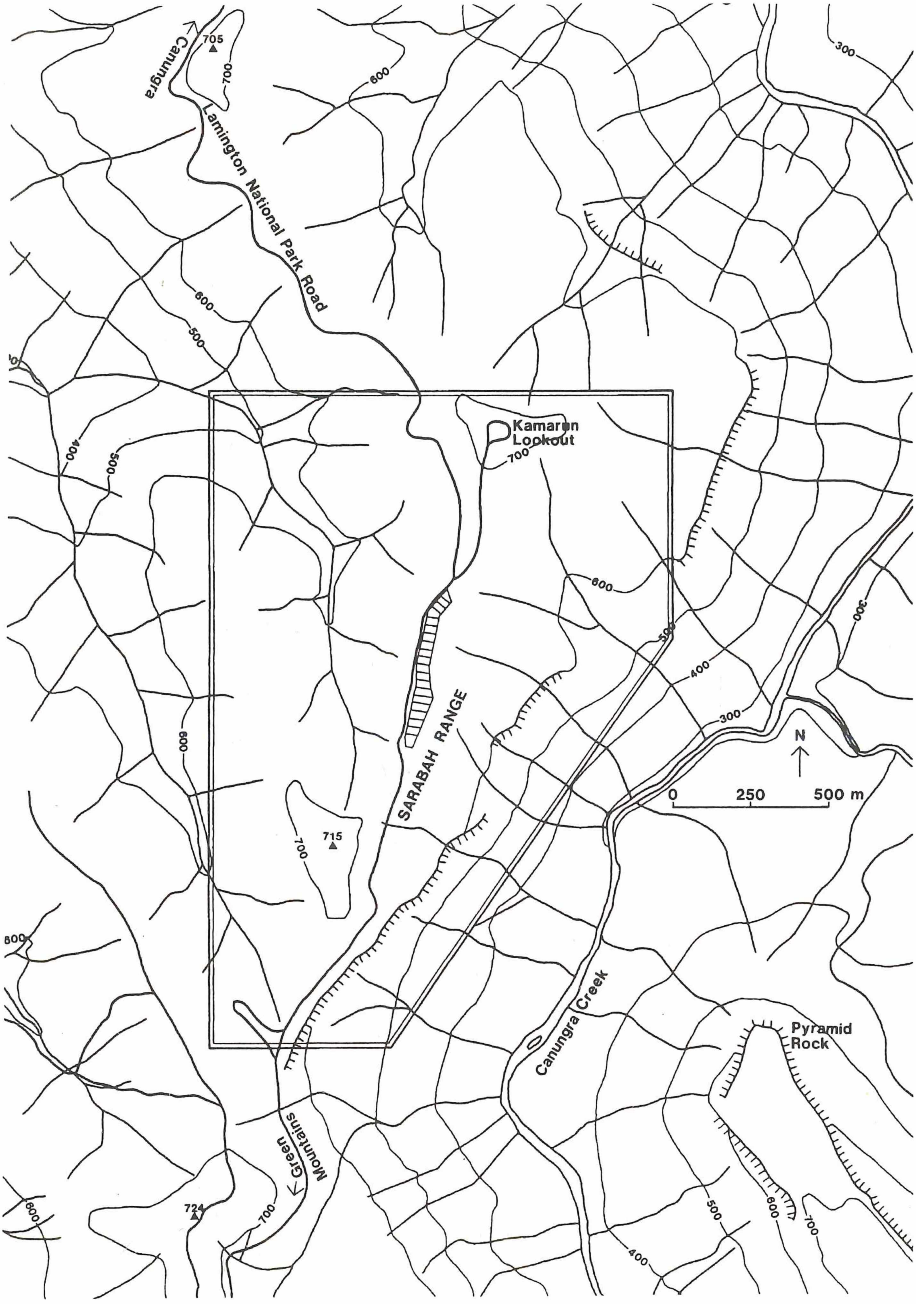
Climate, soil, vegetation and fauna are the four major factors determining the nature of an ecosystem (WALTER & BRECKLE 1983, 1985) and are treated below.

Abiotic factors: climate and soil

The average annual climate may be represented in an ecological climatic diagram (see WALTER & BRECKLE 1983, 1985). The climatic diagram of the study area in the Sarabah Range (see Fig. 2.3) shows a moist subtropical climate, with mean annual rainfall being 1307 mm and mean annual temperature 17.5°C. Rainfall distribution is seasonal, with a wet season in summer and autumn and a dry season in winter and spring. Precipitation is more than 100 mm in seven months of the year.

Figure 2.1 (on page 25). Location of the study area in the central section of the Sarabah Range, marked by the frame. Thick lines represent roads, medium-sized lines represent creeks, thin lines represent contour lines (contour interval 100 metres), and the series of polygons in the centre represents subdivided plots of cleared land.

Abb. 2.1 (auf Seite 25). Lage des Untersuchungsgebiets im mittleren Abschnitt der Sarabah-Bergkette, gekennzeichnet durch den Rahmen. Dicke Linien stellen Straßen dar, mittelgroße Linien stellen Wasserläufe, dünne Linien stellen Höhenlinien (Isohypsen; Isohypsenintervall 100 m) und die Reihe von Vielecken in der Mitte stellt ein in Grundstücke unterteiltes Stück gerodetes Land dar.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Canungra Creek
Pyramid Rock
Green Mountains
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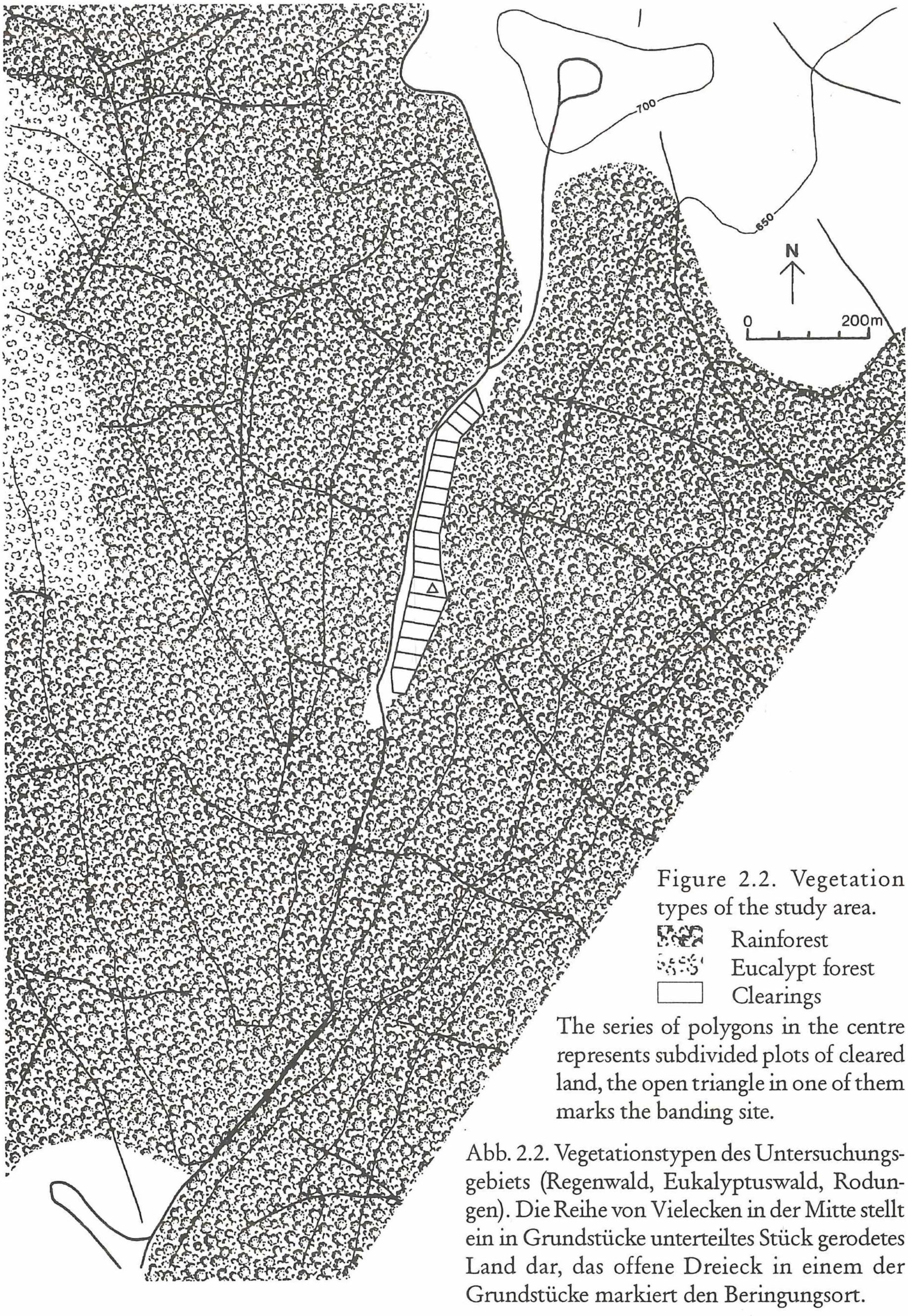

Figure 2.2. Vegetation types of the study area.
▨ Rainforest
░ Eucalypt forest
☐ Clearings
The series of polygons in the centre represents subdivided plots of cleared land, the open triangle in one of them marks the banding site.

Abb. 2.2. Vegetationstypen des Untersuchungsgebiets (Regenwald, Eukalyptuswald, Rodungen). Die Reihe von Vielecken in der Mitte stellt ein in Grundstücke unterteiltes Stück gerodetes Land dar, das offene Dreieck in einem der Grundstücke markiert den Beringungsort.

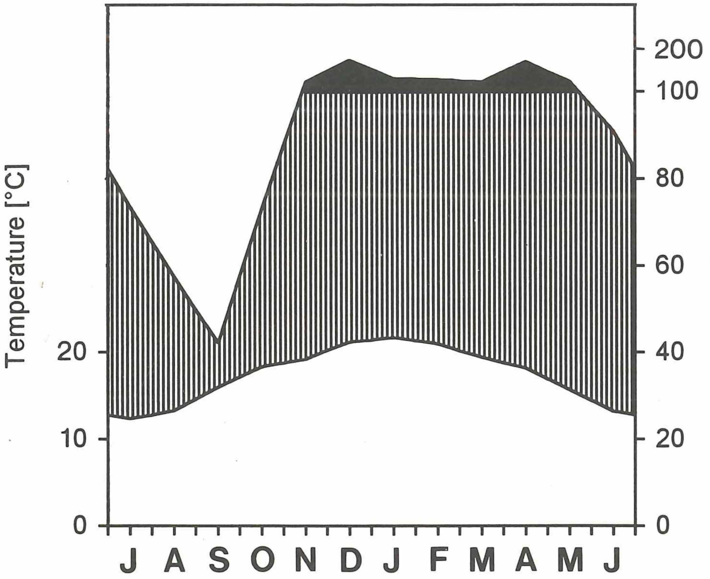

Figure 2.3. Climatic diagram of the Sarabah Range, 660 m above sea level; observations from January 1978 until March 1992. Temperature in °C; rainfall in mm. Mean annual temperature 17.5°C; mean daily minimum during the coldest month 8.3°C; absolute minimum (lowest recorded temperature, 4 July 1984) 0°C; mean daily maximum during the warmest month 26.3°C; absolute maximum (highest recorded temperature, 27 December 1983) 37.5°C. Mean annual rainfall 1307 mm.

Abb. 2.3. Klimadiagramm der Sarabah-Bergkette, 660 m über dem Meeresspiegel; Beobachtungen von Januar 1978 bis März 1992. Temperatur in °C; Niederschlag in mm. Mittlere Jahrestemperatur 17,5°C; mittleres tägliches Minimum des kältesten Monats 8,3°C; absolutes Minimum (tiefste gemessene Temperatur, 4. Juli 1984) 0°C; mittleres tägliches Maximum des wärmsten Monats 26,3°C; absolutes Maximum (höchste gemessene Temperatur, 27. Dezember 1983) 37,5°C. Mittlere jährliche Niederschlagsmenge 1307 mm.

The western slope of the Sarabah Range is exposed to strong, cold and dry westerlies in winter, limiting the expansion of rainforest. The eastern slope is protected, and rainforest vegetation continues through to Darlington Range and Beechmont Range in the east and through to the McPherson Range in the south-east.

Although not visible in the diagram representing the average annual climate (Fig. 2.3), arid periods can occur occasionally. During the three field seasons of this study, from July 1989 until March 1992, such arid periods extended to unusual drought conditions in spring 1990 and spring 1991 (see Fig. 2.4). Moreover, the wet period in between was unusually short and did not fully compensate for the rain deficit. In spring 1991, when

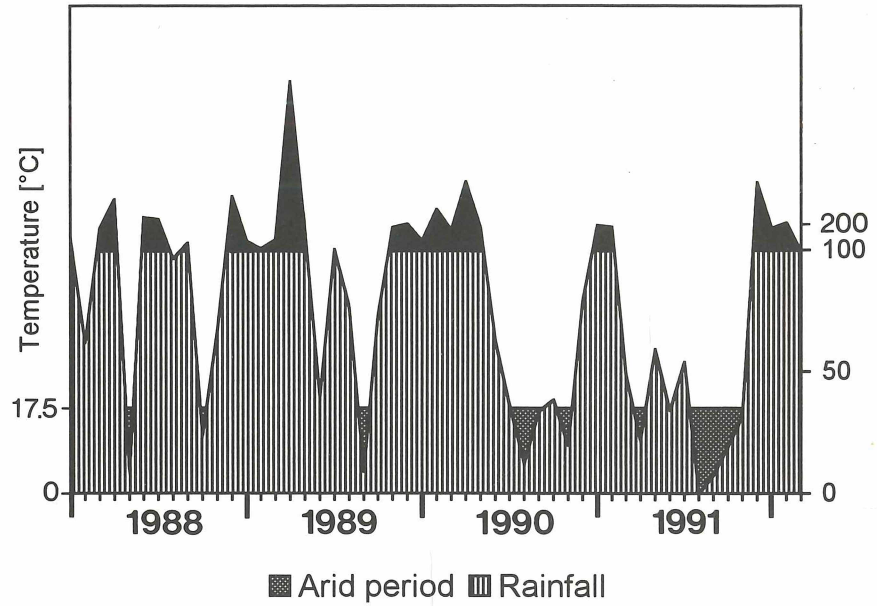

Figure 2.4. Climatic diagram of the Sarabah Range for January 1988 until March 1992 with arid periods in spring 1990 and spring 1991. The mean annual temperature of 17.5°C is shown by the horizontal line.

Abb. 2.4. Klimadiagramm der Sarabah-Bergkette für Januar 1988 bis März 1992 mit Dürrezeiten im Frühling 1990 und Frühling 1991. Die mittlere Jahrestemperatur von 17,5°C wird durch die horizontale Linie gezeigt.

the arid period was even more severe than the one of the previous year, many non-deciduous trees shed leaves and only few produced good fruit crops.

The soils of the Sarabah Range are derived from tertiary basaltic rocks. On the well-drained ridgetop the derived soils are deep krasnozems with red clay subsoils, on the slopes erosion developed shallower brown prairie soils (BECKMANN & THOMPSON 1977). Both are of high fertility (FLOYD 1990).

Biotic factors: vegetation and fauna

The original, natural vegetation of the Sarabah Range consisted of two structurally different types of dry rainforest (McDONALD & WHITEMAN 1979; see Plates 17-18): Araucarian Notophyll Vine Forest on the ridgetop and the more gentle slopes, and Araucarian Microphyll Vine Forest on the steeper and drier slopes (structural-physiognomic classification of WEBB 1959, 1968, 1978). Both are closed forests (height classification of SPECHT 1970, 1981; SPECHT et al. 1974) with more than 70 % projective foliage cover. The total annual rainfall of the Sarabah Range is just at the boundary between dry rainforest and subtropical and warm temperate rainforests (FLOYD 1990); the marked dry season, however, prevents the development of tall closed forest.

In both Araucarian Notophyll Vine Forest and Araucarian Microphyll Vine Forest, Hoop Pines *Araucaria cunninghamii* are the most common emergent trees and woody lianas are abundant. The latter type of rainforest has a lower canopy, often only one tree stratum instead of the usual two strata, smaller leaf-sizes (typically 225-2025 mm^2 instead of 2025-4500 mm^2), fewer plank buttresses, fewer epiphytes, a very sparse herbaceous ground cover, but a well-developed shrub layer, frequently consisting of prickly and thorny species (MCDONALD & WHITEMAN 1979; FLOYD 1990). Typical canopy species of the Araucarian Notophyll Vine Forest are Giant Stinging Tree *Dendrocnide excelsa*, Rose Marara *Pseudoweinmannia lachnocarpa*, Flame Tree *Brachychiton acerifolius* and Lignum-vitae *Premna lignum-vitae*. Typical tree species of the Araucarian Microphyll Vine Forest are Deciduous Fig *Ficus superba* var. *henneana*, Crow's Ash *Flindersia australis*, White Cedar *Melia azedarach* var. *australasica* and Scrub Bottletree or Lacebark Tree *Brachychiton discolor*.

Selective logging took place from the 1930s until the 1950s (JARROTT 1990; A.L. NEALE in litt.), and changed the forest structure and floristic composition of the study area (MCDONALD & WHITEMAN 1979). Emergent Hoop Pines and other sought-after tree species, such as Crow's Ash and Red Cedar *Toona australis*, were removed. Secondary rainforest species, such as Wattles *Acacia* spp., increased in abundance, and naturalized exotic species, such as Common Lantana *Lantana camara*, invaded part of the area. The steeper, less accessible slopes remained largely unaffected, but close to the ridgetop the canopy was opened up, resulting in an uneven canopy in the present areas of regrowth. The latest logging was the clearing of a series of subdivided plots of land on top of the ridge in the early 1960s (A.L. NEALE in litt.).

For a full description of the vegetation of the area see MCDONALD & WHITEMAN (1979) and MCDONALD & THOMAS (1989). A list of the vascular plant species of the study area is given in Appendix 1.

Although logging has adversely influenced the vegetation of the study area, its fauna is still diverse. The mammal fauna includes Mountain Brushtail Possum *Trichosurus caninus*, Long-nosed Potoroo *Potorous tridactylus*, Red-legged Pademelon *Thylogale stigmatica* and Red-necked Pademelon *T. thetis*. The avifauna contains most species characteristic of rainforests in south-eastern Queensland (see FRITH 1977; STORR 1984; NIELSEN 1991), including Noisy Pitta *Pitta versicolor*, Albert's Lyrebird *Menura alberti*, Rose Robin *Petroica rosea*, Logrunner *Orthonyx temminckii*, Eastern Whipbird *Psophodes olivaceus*, Paradise Riflebird *Ptiloris paradiseus* and three members of the bowerbird family: the monogamous Green Catbird *Ailuroedus crassirostris* and the bower-building Regent and Satin Bowerbirds. A list of the bird assemblage of the study area is given in Appendix 2.

2.2 Methods

This study is mainly based on field observations of the Regent Bowerbird population in the Sarabah Range, conducted over 33 months, from July 1989 until March 1992. In addition to the data obtained through field work, Chapters 3 and 5 are partly based on materials examined in zoological collections and on data provided by the Australian Bird and Bat Banding Schemes (ABBBS), and Chapter 8 is mainly based on data from oological collections. The museum work was carried out between 1990 and 1998.

The field work in the Sarabah Range involved trapping, colour banding and measuring of all Regent Bowerbirds of the study population, systematic searches for their bowers, hide-based observations of bower activities, and more opportunistic observations of foraging birds throughout the study area.

A total of 203 Regent Bowerbirds was trapped during the three years of field work. All birds were caught with a drop trap, operated in the centre of the study area. The banding site (see Fig. 2.2) was the place where author and research assistants were living, an ideal arrangement which made it possible to operate the trap and to conduct field work almost daily and, consequently, to maintain a totally-banded population.

The drop trap in use was a simple fall trap and was sprung with a prop and pullstring (see BUB 1991). The wooden frame measured 90 cm x 90 cm, the cover of the top was made of chicken wire and had a height of 10 cm. The trap was baited with fruit, usually bananas. All 203 trapped individuals, 101 males and 102 females, were banded with a numbered metal band (magnesium-aluminium alloy) from the Australian National Parks and Wildlife Service and with an individual combination of three colour bands (Darvic PVC) from the Australian Bird Study Association.

The colour-banding schema in use was recommended by LOWE (1989) for individual recognition of known sedentary species not being studied by other banders. The band positions were two colour bands on the left tarsus (tarsometatarsus) and one colour band over the metal band on the right tarsus (colour-banding schema 3 in LOWE 1989). Six colours were used: red, black, dark blue, light green, orange and white. Combinations of three of the six colours allowed $6^3 = 216$ individual combinations. The six colours were recommended by LOWE (l.c.) because they did not fade strongly in trials where they were exposed to natural weather conditions for more than a year.

Individual birds were designated by their colour band combinations using the following abbreviations: R for red, N for black, B for dark blue, G for light green, O for orange and W for white colour bands. As every bird was marked with three colour bands, it was designated by a combination of three letters, the first denoting the colour band over the metal band on the right tarsus, the second denoting the upper band on the left tarsus, and the third letter denoting the lower band. A list of all colour band combinations with banding details is given in Appendix 3.

Colour bands may influence the reproductive behaviour and success of birds (BURLEY et al. 1982). In order to avoid this possible effect, orange bands were not used for colour-banding male Regent Bowerbirds, because this colour resembles the colour of crown, nape and wings of adult males, and because it was observed that they remove orange-coloured leaves from their bowers. A few males however were banded with band combinations including orange because of temporary unavailability of some other colours in the required band size, but none of these individuals featured in observations of reproductive behaviour.

Every trapped bird was measured and weighed, and a detailed description of plumage and unfeathered parts was taken. Several thousand sightings of the colour-banded birds were recorded. Furthermore, more than one hundred re-traps were made, predominantly to examine and measure birds which had changed plumage. Catching, banding and colour marking was carried out under Australian Bird and Bat Banding Schemes banding and colour marking authority number 1583 and under Queensland National Parks and Wildlife Service banding permits 1989-T471, 1990-B256 and 1991-B292.

Birds were observed with two different pairs of binoculars, a Zeiss Dialyt 10x40 B and a Hensoldt Diagon 8x30. The latter have a shorter minimal focusing distance, which often proved to be an advantage during observations from hides. Two prefabricated Jansport observation hides were used (height 160 cm; width 100 cm; length 150 cm). The hides could be taken to any part of the study area very quickly and were erected within ten minutes.

In Australia, a mating and breeding season spans two calendar years and, following ROWLEY et al. (1991), is referred to by the year in which it started. For example, the 1989 season ran from August 1989 to February 1990.

Means are expressed as mean ± one standard deviation (*s.d.*). Levels of significance, P, are given as: * = $0.05 > P > 0.01$, ** = $0.01 > P > 0.001$, *** = $P < 0.001$, *n.s.* = not significant. All other methods and terminology are described in separate sections of the chapters treating the aspects of the study for which they were important.

3 Morphology and Plumage: Sex-related, Age-related and Geographical Variation

3.1 Introduction

In many bird species males and females differ in plumage colouration or body size, a phenomenon referred to as sexual dimorphism (BROOKE & BIRKHEAD 1991; DE JUANA 1992). It may already have existed in birds more than 120 million years ago (ACKERMAN 1998; cf. PETERS & QIANG 1999).

DARWIN (1871) considered sexual dimorphism of birds to have evolved through two modes of sexual selection: male-male competition for females favouring males with large size, and female choice favouring males with bright plumages and/or vigorous displays. In most bird species that are sexually dimorphic in plumage, males are more brightly coloured than females, the opposite mainly occurring in the few species with polyandrous mating systems (ORING 1982; BEZZEL & PRINZINGER 1990; PERRINS 1990; BROOKE & BIRKHEAD 1991; DE JUANA 1992; JOHNSGARD 1994).

PAYNE (1984) reviewed sexual size dimorphism in bird species with different mating systems and found that in most species with polygynous mating systems males are larger than females. However, it was impossible to explain all variation in sexual dimorphism with differences in the mating system, because some monogamous species are also dimorphic, and sexual size dimorphism also varies with overall body size among species (PAYNE l.c.).

In addition to sexual selection, a number of other factors are likely to have influenced differences in adult morphology and plumage between and within species. BERGMANN's (1847) zoogeographical rule states that members of a taxon are smaller in warmer environments than in cooler parts of their range. In closely-related species of passerine birds, long distance migrants often have longer and more pointed wings than short distance migrants (KIPP 1959; BEZZEL & PRINZINGER 1990). Morphological differences between the adult sexes of a species may also be related to intersexual differences in foraging (SELANDER 1966, 1972).

In the bowerbird family, species of the only monogamous genus *Ailuroedus* are sexually monomorphic in plumage, but in the non-monogamous genera no consistent trend in adult plumage dimorphism is found: for example, all *Sericulus* species are markedly dimorphic, whereas *Chlamydera* species are only slightly dimorphic or monomorphic (COOPER & FORSHAW 1977; DONAGHEY et al. 1985; FRITH & FRITH 1998a). According to PAYNE (1984), sexual dimorphism in size is no greater in the non-monogamous bowerbirds than in the monogamous catbirds.

There are few studies on variation of morphology and plumage in the bowerbird family, and these are not comprehensive. MAYR & JENNINGS (1952) studied plumages and geographical variation in Australian bowerbird species but restricted their analysis to specimens from American museums. According to KEAST (1961), clinal variation occurs in several Australian bowerbird species, including the Regent Bowerbird, but no further details are given. PAYNE (1984) included the bowerbird family in his review but limited his data source to the measurements given by COOPER & FORSHAW (1977). This source lists only the range of wing, culmen and tarsus measurements in male and female bowerbirds, but does not give sample sizes, means and standard deviations, and does not consider geographical variation.

Published information on variation of morphology and plumage in the Regent Bowerbird is fragmentary and partly contradictory. Most authors agree that, in contrast to the majority of bird species in which males compete for multiple mating opportunities, male Regent Bowerbirds are considerably smaller than females (MAYR & JENNINGS 1952; DISNEY & LANE 1971; DISNEY 1971, 1974; COOPER & FORSHAW 1977). PAYNE (1984, pp. 37-38), however, called this species "the least size-dimorphic bowerbird".

MATHEWS (1912) separated a subspecies *S. c. rothschildi* on the basis of brighter colouring of adult males from the Blackall Range. MAYR & JENNINGS (1952) found adult males from both Blackall Range and Bunya Mountains more richly coloured on crown and nape than birds from New South Wales, and concluded that it is thus perhaps justifiable to recognize *rothschildi*. On the other hand, COOPER & FORSHAW (1977) stated that this form is probably not separable from the nominotypical *S. c. chrysocephalus*.

Adult males of the *Sericulus* species, the Australian Regent Bowerbird and the Flame and Fire-maned Bowerbirds from New Guinea, are the most colourful of all bowerbirds. While the adult males of these species are unmistakable, correct identification of the sex and age of 'brown' birds, i.e. females and immature males, is very difficult. For example, according to MAYR & JENNINGS (1952), adult female Regent Bowerbirds and immatures of both sexes have approximately the same measurements of wing and tail feathers, but according to DISNEY & LANE (1971) and DISNEY (1971, 1974) their measurements differ.

The sequences of moult and changes in plumages of the Regent Bowerbird are poorly known. Males attain full adult plumage in their third year according to GOULD (1865), their fourth or fifth year according to PHILLIPPS (1901-1911), their fifth or sixth year according to DISNEY & LANE (1971) and their seventh year according to SINDEL (1989). VELLENGA's (1980a) detailed study on moult sequences and plumage changes of the Satin Bowerbird is the only such work on any bowerbird species. Male Satin Bowerbirds attain full adult plumage in their seventh year, whereas females do not change plumage colour from their third year on (VELLENGA l.c.). As both Satin and Regent Bowerbirds are sexually dimorphic in plumage, and as the two species are closely related, it may be expected that the moult sequences of the two species are similar.

Regent and Satin Bowerbirds occur together over much of their ranges (BLAKERS et al. 1984) and build similar avenue bowers (see Figs 1.2d-e and Plates 6 and 12). It has been suggested that competition between the two species has been an important factor in their evolution (GILLIARD 1969; BARDEN 1977; see Chapter 6). The ranges of the *Sericulus* species in New Guinea do not overlap with closely-related species to the extent found in

Regent and Satin Bowerbirds (Coates 1990). Therefore, a comparison of all *Sericulus* species should reveal any differences in their morphology and plumage that may be due to the presence or absence of other bowerbirds.

In any study of behaviour and ecology of an animal species it is important to know the sex and age of the individuals observed. Therefore, it is the main aim of this chapter to describe morphology and plumage of the Regent Bowerbird as a guide to determining the sex and age of individuals of this species. Sex- and age-related variation is compared with geographical variation and with those of the congeneric Flame and Fire-maned Bowerbirds to assess factors which may have influenced morphological differences in the evolution of the species.

3.2 Materials and methods

Considerable efforts were made to uncover potential sources of data on morphology and plumage of the *Sericulus* species. In addition to the Regent Bowerbird data collected in the Sarabah Range (see Chapter 2), *Sericulus* study skins and museum mounts were examined and measured in zoological collections in Australia and Europe (see Appendix 4). The ABBBS provided morphometric measurements of Regent Bowerbirds banded by other bird banders and filed on microfiches (see Appendix 5). No Flame and Fire-maned Bowerbirds have been banded to date, but some additional measurements were obtained from Chapin (1929), Gilliard & LeCroy (1967) and Diamond (1969).

Together, these data sources constituted measurements of 1044 *Sericulus* individuals: 910 Regent Bowerbirds (203 individuals banded in the study area, 346 museum specimens and 361 individuals banded by other bird banders), 121 Flame Bowerbirds (86 museum specimens and 35 from the literature) and 13 Fire-maned Bowerbirds (1 museum specimen and 12 from the literature).

Detailed descriptions of plumage and unfeathered parts were made. Morphometric measurements were taken using calipers, butted and flat rulers, and Pesola spring balances. All measuring methods used are explained in Table 3.1. Most measurements were taken in accordance with the recommendations of the Australian Bird Bander's Manual (Lowe 1989), the bill measurements were taken in accordance with Disney (1971, 1974). In the analysis of data on Regent Bowerbirds, some sample sizes are well below the 910 individuals mentioned above, because other bird banders took only few measurements.

For the study of geographical variation, subspeciation has to be considered. In both Regent and Flame Bowerbirds two subspecies have been described. Only slight differences in colour intensity of adult males have been found across populations of the Regent Bowerbird (Mathews 1912; Mayr & Jennings 1952). In contrast, the Flame Bowerbird exists in two well-differentiated taxa, *S. a. aureus* and *S. a. ardens*, presently treated as subspecies (Coates 1990). These differences in the degree of subspeciation and the differences in the sample sizes were taken into account when specimens of the two

Table 3.1. Measuring methods used for collecting morphometric data from live and skinned *Sericulus* specimens. The traits total length and wing span were only taken of live birds.
Tab. 3.1. Vermessungsmethoden zur Erfassung morphometrischer Daten von lebenden *Sericulus*-Individuen und von Balgmaterial. Die Merkmale 'total length' (Gesamtlänge) und 'wing span' (Spannweite) wurden nur von lebenden Vögeln erfasst.

Measure	Method
Body mass	The bird was weighed in a cloth bag, and its body mass found by subtracting the mass of the bag from the total mass measured.
Total length	The bird was placed flat on its back on a ruler with its head bent backwards, and the maximum distance between the tip of the bill and the tip of the longest tail feather was measured.
Wing span	The bird was placed on its back on a ruler with the wings spread and held open, and the maximum distance from wing tip to wing tip was measured.
Wing length	The carpal joint (carpus) was placed against the butt of a ruler, and the outer flight feathers of the wing (outer remiges or primaries) were flattened and straightened on the ruler to give the maximum measurement (maximum wing chord).
Tail length	The maximum distance from the point of entry of the shafts of the central flight feathers of the tail (rectrices) into the skin to the tip of the longest tail feather was measured.
Head-bill length	The maximum distance between the tip of the bill and the back of the head was measured.
Head depth	The maximum dorso-ventral head dimension was measured from the middle of the bird's throat to the point vertically on top of its head.
Head width	The maximum lateral head dimension was measured at the widest part of the head just behind the eyes.
Bill length	The distance between the tip of the bill and the anterior margin of the skull was measured.
Bill depth (nostrils and base)	The bill depth was measured from directly above the distal end of the nostrils (nares) to the ventral edge of the lower mandible directly below (bill depth nostrils) and at the base of the exposed culmen (bill depth base).
Bill width (nostrils and gape)	The bill width was also measured at the distal end of the nostrils (bill width nostrils) and at the point where the upper mandible meets the lower (bill width gape).
Tarsus length	The tarsus (properly called the tarsometatarsus) length was measured from the intertarsal joint to the distal end of the last undivided scale before the toes diverge.
Tarsus length with foot	The foot was bent downwards, and the distance between the intertarsal joint and the distal end of the tarsus was measured.
Tarsus plus middle toe length	The leg was laid flat on a ruler with the proximal end of the tarsus placed against the butt, and the distance to the distal end of the flattened middle toe (without claw) was measured.
Tarsus width (maximum)	The tarsus width was measured as the anterior-posterior diameter of the tarsus at its mid-point (tarsus width) and at the point where the maximum width of the tarsus occurs (tarsus width maximum).

species were separated into pools of regional populations: Regent Bowerbird specimens were separated into seven pools of populations along the eastern Australian distribution of the species (see Table 3.4); Flame Bowerbird specimens were separated into the two distinct taxa, *aureus* in northern and western New Guinea and *ardens* in southern and south-western New Guinea (see Table 3.9). The Fire-maned Bowerbird has a limited range (see Fig. 3.1) and was not separated into regional populations.

Student's *t*-tests were used to test differences between the means of any pair of two samples (SPATZ & JOHNSTON 1989).

3.3 Results

3.3.1 Regent Bowerbird

Sex-related and age-related variation in morphology

Morphological measurements of male and female Regent Bowerbirds are summarized in Table 3.2. The species shows substantial sexual dimorphism in body size, with males being smaller than females. Of the 18 traits analysed, males were highly significantly smaller than females in 14 ($P < 0.001$ for all 14 traits). The highest level of significance was found in the differences of bill width nostrils, bill depth nostrils, wing length, tail length and body mass (in this order). Measurements of these dimorphic traits are most important when determining the sex of females and immature males, which do not show sex-related differences in plumage.

The mean bill length, however, was slightly larger in males than in females ($P < 0.02$). But the bill length measurements of male and female Regent Bowerbirds showed much overlap.

Differences in wing and tail measurements between adult males, immature males and females are summarized in Table 3.3. Wing span, wing length and tail length of immature males were significantly longer than those of adult males and significantly shorter than those of females, although ranges overlap slightly.

Sex-related and age-related variation in plumage

Male Regent Bowerbirds attain adult plumage considerably later than females. The period of three years of field work was not long enough to follow all changes in plumage and unfeathered parts of individual males from hatching until attaining full adult plumage. However, it was possible to investigate the pattern of changes through regular observations and re-traps of individuals of different ages.

Down plumage: All species in the bowerbird family are altricial and nidicolous. Nestlings of Regent Bowerbirds have soft and fluffy, grey down feathers and a bright orange gape (see photographs in DISNEY & LANE 1971; CHAFFER 1984; THRELFO 1985; SINDEL 1989).

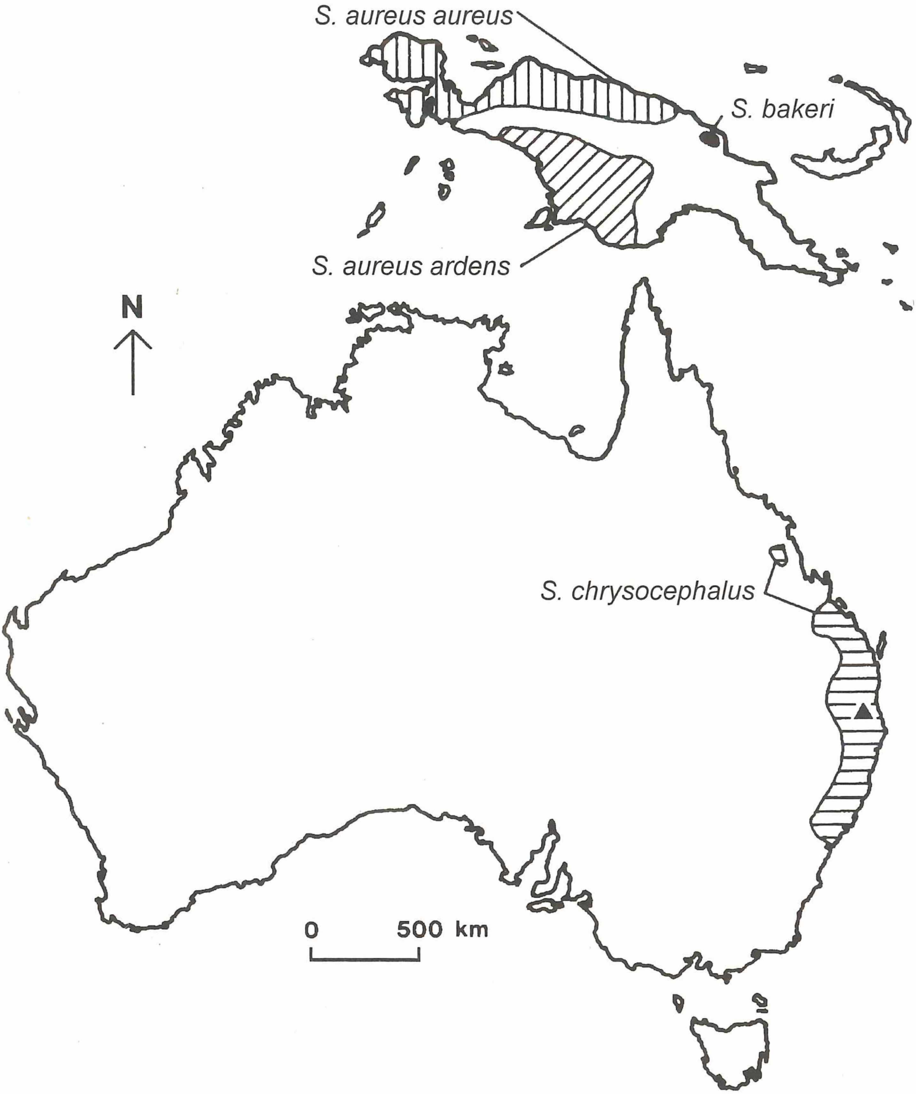

Figure 3.1. Distribution of the genus *Sericulus* (modified from maps in DIAMOND 1969; GILLIARD 1969; BELL 1970; COOPER & FORSHAW 1977; BLAKERS et al. 1984; COATES 1990): Flame Bowerbird *S. aureus aureus* and *S. aureus ardens*, Fire-maned Bowerbird *S. bakeri* and Regent Bowerbird *S. chrysocephalus*. The black triangle marks the location of the study area in the Sarabah Range.
Abb. 3.1. Verbreitung der Gattung *Sericulus* (modifiziert nach Karten in DIAMOND 1969; GILLIARD 1969; BELL 1970; COOPER & FORSHAW 1977; BLAKERS et al. 1984; COATES 1990): Goldlaubenvogel *S. aureus aureus* und *S. aureus ardens*, Rotscheitel-Laubenvogel *S. bakeri* und Gelbnacken-Laubenvogel *S. chrysocephalus*. Das schwarze Dreieck markiert die Lage des Untersuchungsgebiets in der Sarabah-Bergkette.

Table 3.2. Morphometric comparison of male (adults and immatures) and female Regent Bowerbirds for traits as defined in Table 3.1. Body mass is in g, all other measures are in mm.
Tab. 3.2. Morphometrischer Vergleich von männlichen (adulten und immaturen) und weiblichen Gelbnacken-Laubenvögeln für Merkmale wie in Tab. 3.1 definiert. Körpermasse ('body mass') in g, alle anderen Maße in mm.

Measure	Sex	Mean ± *s.d*	*n*	*t*	*P*
Body mass	Male	97.7 ± 8.3	223	19.45	$< 0.001^{***}$
	Female	115.8 ± 11.0	211		
Total length	Male	265.5 ± 13.3	52	5.49	$< 0.001^{***}$
	Female	279.8 ± 10.0	36		
Wing span	Male	420.8 ± 13.4	111	11.83	$< 0.001^{***}$
	Female	439.8 ± 10.6	114		
Wing length	Male	131.2 ± 3.9	450	21.95	$< 0.001^{***}$
	Female	137.5 ± 3.5	279		
Tail length	Male	93.6 ± 9.0	371	21.03	$< 0.001^{***}$
	Female	107.9 ± 3.9	189		
Head-bill length	Male	57.0 ± 3.7	223	0.83	*n.s.*
	Female	57.4 ± 1.7	72		
Head depth	Male	23.4 ± 4.0	176	0.39	*n.s.*
	Female	23.2 ± 1.3	47		
Head width	Male	22.7 ± 1.5	186	3.37	$< 0.001^{***}$
	Female	23.6 ± 1.8	52		
Bill length	Male	26.0 ± 2.4	394	2.41	$< 0.02^{*}$
	Female	25.6 ± 2.1	220		
Bill depth nostrils	Male	7.1 ± 0.3	420	33.09	$< 0.001^{***}$
	Female	7.9 ± 0.4	232		
Bill depth base	Male	7.9 ± 0.4	227	15.70	$< 0.001^{***}$
	Female	8.9 ± 0.5	68		
Bill width nostrils	Male	5.9 ± 0.3	419	34.24	$< 0.001^{***}$
	Female	6.9 ± 0.4	230		
Bill width gape	Male	9.6 ± 0.7	231	13.06	$< 0.001^{***}$
	Female	10.8 ± 0.7	68		
Tarsus length	Male	35.5 ± 1.4	256	7.44	$< 0.001^{***}$
	Female	36.6 ± 1.2	121		
Tarsus length with foot	Male	37.4 ± 1.2	270	8.63	$< 0.001^{***}$
	Female	38.5 ± 1.3	135		
Tarsus plus middle toe length	Male	59.5 ± 4.2	48	1.07	*n.s.*
	Female	60.8 ± 4.2	14		
Tarsus width	Male	3.8 ± 0.2	287	14.79	$< 0.001^{***}$
	Female	4.2 ± 0.2	152		
Tarsus width maximum	Male	4.4 ± 0.3	287	13.72	$< 0.001^{***}$
	Female	4.8 ± 0.3	153		

Table 3.3. Comparison of wing and tail measurements of adult male, immature male and female Regent Bowerbirds. All measures are in mm.

Tab. 3.3. Vergleich der Flügel- und Schwanzmaße von adulten männlichen, immaturen männlichen und weiblichen Gelbnacken-Laubenvögeln. Alle Maße in mm.

Measure	Sample	Mean ± *s.d.*	*n*	*t*	*P*
Wing span	Adult male	415.7 ± 12.2	40		
				3.14	$< 0.003^{**}$
	Immature male	423.7 ± 13.3	71		
				9.14	$< 0.001^{***}$
	Female	439.8 ± 10.6	114		
Wing length	Adult male	128.8 ± 3.0	223		
				16.16	$< 0.001^{***}$
	Immature male	133.6 ± 3.3	227		
				12.99	$< 0.001^{***}$
	Female	137.5 ± 3.5	279		
Tail length	Adult male	86.2 ± 3.1	203		
				41.09	$< 0.001^{***}$
	Immature male	102.4 ± 4.5	168		
				12.30	$< 0.001^{***}$
	Female	107.9 ± 3.9	189		

Juvenile plumage: The grey down plumage is replaced by brown juvenile plumage through a post-natal moult. Juvenile body feathers are soft and loosely textured, but in colouring resemble the brown speckled plumage of older birds in both sexes. Irides of juveniles are dark brown, the bill is blackish. Tarsi (tarsometatarsi) of juveniles are light grey, much lighter than the brownish-black tarsi of older birds. Two nestlings observed while fledging (see Chapter 8) had still retained down feathers on crown, nape and mantle.

First-year plumage: The juvenile body plumage is retained only for a few weeks. While remiges and rectrices are still growing, the soft juvenile body plumage is replaced by stiffer contour feathers through a post-juvenile moult. Remiges and rectrices are not replaced during this incomplete moult. When fully grown, the rectrices of first-year birds are more pointed than those of older birds (see Fig. 3.2). Irides are still dark brown, bill blackish, tarsi light grey.

Second-year plumage: The first-year plumage is replaced by second-year plumage through the first annual moult. The second-year plumage of both sexes essentially looks like first-year plumage, but the rectrices are less pointed than those of younger birds (see Fig. 3.2). This is the last noticeable age-related change in the plumage of females (see Plate 19). Irides of both sexes are still dark brown, the bill is still blackish, but the tarsi are brownish-black, darker than the tarsi of younger birds. The first annual moult begins in late winter, when the birds are slightly more than half a year old; the first annual moult seems to be less seasonal and to take longer than the later yearly moults.

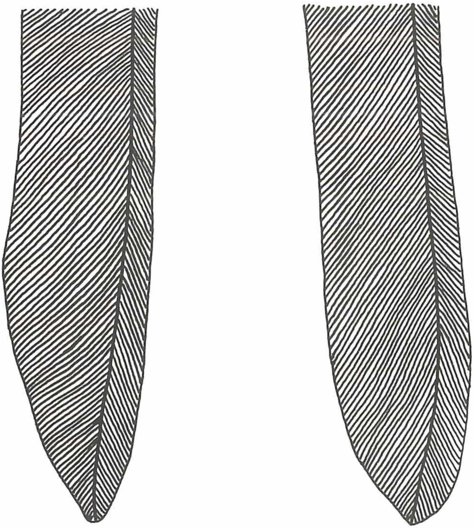

Figure 3.2. Rectrices (flight feathers of the tail) of 'brown' (female-plumaged) Regent Bowerbirds. In both sexes rectrices of first-year birds (on the left) are more pointed, those of second-year and of older birds (on the right) are less pointed (drawn from photographs taken of museum specimens).

Abb. 3.2. Rectrices (Steuerfedern) von 'braunen' (weibchenfarbenen) Gelbnacken-Laubenvögeln. Bei beiden Geschlechtern sind die Rectrices von Vögeln im ersten Lebensjahr (links) stärker zugespitzt, jene von Vögeln im zweiten Lebensjahr und von älteren Vögeln (rechts) sind weniger zugespitzt (nach Fotografien von Museumsbälgen gezeichnet).

Third-year plumage (males): Third-year plumage is attained through the second annual moult and looks like second-year plumage. In third-year males irides and bill commence to change colour (see Plate 20). Irides are lighter brown mottled with yellowish spots, and the bill is dark brownish with lighter stripes.

Fourth-year and fifth-year plumages (males): In the fourth and fifth year the plumage still looks like second-year plumage. However, in males iris colour gradually changes to yellow and bill colour changes from dark brown over light brown to orange-brown (see Plates 21-22).

Sixth-year plumage (males): When in sixth-year plumage, most males have almost completely yellow irides and an orange bill (see Plate 23). In some males irides still show a few brown spots and the bill still shows some brown stripes, predominantly at the base. Most of the sixth-year plumage is still brown, but black and yellow feathers of the adult plumage may appear in individually different numbers (see Plate 24).

Seventh-year plumage (males): With their sixth annual moult males attain complete adult plumage (see Fig. 3.3 and Plate 25). Irides are bright yellow and the bill is orange, though in some males the base of the bill still shows small brown stripes.

Individual variation

Plumages of female and immature male Regent Bowerbirds show considerable individual, not sex- or age-related, variation: the extent of their dark crown and throat varies greatly; females and immature males of all ages may have some, up to several dozen, yellow feathers on the nape, more rarely on the crown; some females and immature males may also have a few partly yellow remiges.

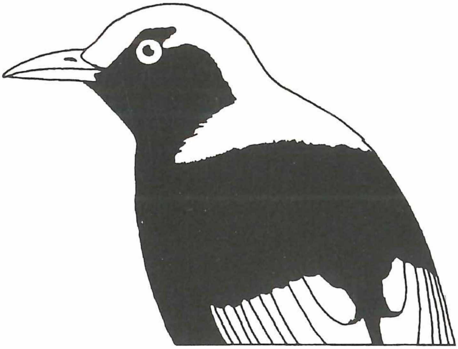

Figure 3.3. Portrait of an adult male Regent Bowerbird (drawn after a painting by WILLIAM T. COOPER in COOPER & FORSHAW 1977).
Abb. 3.3. Porträt eines adulten männlichen Gelbnacken-Laubenvogels (gezeichnet nach einem Bild von WILLIAM T. COOPER in COOPER & FORSHAW 1977).

Out of 102 females banded in the Sarabah Range, five had irides mottled with yellowish spots and four had a lighter brown area on the upper mandible of the otherwise blackish bill. The females already showed these traits when examined for the first time during banding and did not look different when re-trapped later. Therefore, it is unknown when the slight changes in iris and bill colour had occurred. Presumably, these changes had not occurred until the females′ third year of life, because none of the definite first-year and second-year females showed such changes. Whereas the change in the iris colour may lead to almost completely yellow irides (see photographs in DISNEY & LANE 1971; CHAFFER 1984), none of the 181 females examined (102 females examined in the Sarabah Range and 79 female museum specimens) showed more than small paler areas on the bill. For example, on the label of female museum specimen MVHLW 6406 (see Appendix 4 for institution abbreviations) "eyes gold yellow mottled with brown" had been noted by the collector, but this female nevertheless had a completely black bill.

The change of iris and bill colour in immature males also varies individually: in most males iris colour changes more quickly than bill colour, but in some males it is the reverse. In sixth-year plumage some males show a few partly yellow remiges, a few completely black rectrices and/or partly adult plumage on the head. In adult plumage, some males show yellowish shafts and/or a small yellow patch at the caudal end of the otherwise black rectrices.

Despite all irregularities in the colour changes of males, the following general pattern was observed: males show a brown plumage, brown irides and black bill for two years, and for another four years they show an at least predominantly brown plumage, while iris and bill colour are changing. Therefore, the first adult plumage of male Regent Bowerbirds must be their seventh-year plumage, attained through their sixth annual moult. However, some males were observed in partly adult plumage outside the moulting season (see Plate 24), whereas other males acquired complete adult plumage in a single moult. This suggests that not all males attain adult plumage at the same age.

Geographical variation

Seven pools of regional populations of Regent Bowerbirds, separated to analyse geographical variation, are defined in Table 3.4. Wing length measurements of adult males, immature males and females of these pools of populations are compared in Table 3.5 as an indicator of overall size.

Table 3.4. Seven pools of regional populations of Regent Bowerbirds, lettered A to G (N to S), separated to analyse geographical variation. Location, elevation above sea level and predominant types of vegetation of the seven areas.
Tab. 3.4. Sieben 'Pools' regionaler Populationen des Gelbnacken-Laubenvogels - mit den Buchstaben A bis G bezeichnet (von N nach S) -, die zur Analyse von geographischer Variation unterschieden wurden. Fundorte, ihre Höhe über dem Meeresspiegel und vorherrschende Vegetationstypen der sieben Bereiche.

Area	Location of area	Elevation and vegetation
A	Latitude 21°02'-21°08'S Clarke Range west of Mackay	500-900 m above sea level Tropical upland rainforest
B	Latitude 24°18'-27°28'S South-eastern Queensland ranges (Many Peaks Range, Dawes Range, Blackall Range, Conondale Range, Bunya Mountains, D'Aguilar Range)	200-700 m above sea level Subtropical foothill and upland rainforest
C	Latitude 28°10'-28°14'S Northern Border Ranges (Sarabah Range and McPherson Range)	600-900 m above sea level Subtropical, dry and warm temperate rainforest
D	Latitude 28°20'-28°41'S North-eastern New South Wales ranges (Tooloom Range, Richmond Range, Tweed Range)	200-700 m above sea level Subtropical and warm temperate rainforest
E	Latitude 29°24'-29°25'S Iluka Nature Reserve	0-10 m above sea level Littoral rainforest
F	Latitude 30°26'-32°18'S New England area (Bellinger River, Nambucca River) and Barrington-Gloucester area (Manning River, Chichester River, Allyn River)	400-700 m above sea level Subtropical and cool temperate rainforest
G	Latitude 32°56'-33°28'S Newcastle-Gosford area (Blackbutt Reserve, Tumbi Umbi, Kincumber)	0-100 m above sea level Wet sclerophyll forest

The wing length measurements of the seven population pools showed differences which conform with BERGMANN's (1847) zoogeographical rule. Adult males, immature males and females were smallest in the northernmost population (area A) but samples were unfortunately small. In the southern part of their geographical distribution, Regent Bowerbirds were smaller in lowland areas (areas E and G) than in mountain ranges (areas C and D). Despite the size differences between populations, in all seven populations males were smaller than females, and immature males were intermediate in size between adult males and females.

The examination of museum specimens did not show geographical variation in the plumages of immature males (81 specimens examined) and females (79 specimens examined). In adult males (186 specimens examined), however, slight differences in the intensity of the orange-yellow crown and nape were noticeable. All adult males with a brighter colouring came from the northern part of the range (e.g., MVHLW 1114 from Mackay, QM 9111 from the Many Peaks Range, MV B2036 from the Bunya Mountains and QM 16907 from the McPherson Range).

Table 3.5. Comparison of wing length measurements (in mm) of the seven pools of regional populations of Regent Bowerbirds (A to G) defined in Table 3.4.

Tab. 3.5. Vergleich der Flügellängen (in mm) der sieben in Tab. 3.4 definierten 'Pools' regionaler Populationen des Gelbnacken-Laubenvogels (A bis G).

Sample		A	B	C	D	E	F
Adult males:							
A	124.5 ± 0.7 (n = 2)						
B	129.7 ± 2.8 (n = 26)	*					
C	129.7 ± 2.6 (n = 33)	**	*n.s.*				
D	129.2 ± 3.1 (n = 39)	*	*n.s.*	*n.s.*			
E	125.4 ± 2.4 (n = 17)	*n.s.*	***	***	***		
F	127.9 ± 2.9 (n = 14)	*n.s.*	*n.s.*	*	*n.s.*	*	
G	129.5 ± 3.8 (n = 17)	*n.s.*	*n.s.*	*n.s.*	*n.s.*	***	*n.s.*
Immature males:							
A	129.2 ± 1.8 (n = 2)						
B	134.3 ± 2.7 (n = 12)	*					
C	135.4 ± 2.8 (n = 71)	**	*n.s.*				
D	133.8 ± 3.2 (n = 18)	*n.s.*	*n.s.*	*			
E	132.0 ± 3.0 (n = 46)	*n.s.*	*	***	*		
F	132.7 ± 2.9 (n = 7)	*n.s.*	*n.s.*	*	*n.s.*	*n.s.*	
G	132.7 ± 3.1 (n = 44)	*n.s.*	*n.s.*	***	*n.s.*	*n.s.*	*n.s.*
Females:							
A	134.7 ± 1.2 (n = 3)						
B	137.4 ± 2.7 (n = 9)	*n.s.*					
C	139.0 ± 3.4 (n = 98)	*	*n.s.*				
D	137.7 ± 3.6 (n = 23)	*n.s.*	*n.s.*	*n.s.*			
E	135.6 ± 2.3 (n = 51)	*n.s.*	*	***	**		
F	137.3 ± 2.8 (n = 10)	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*	
G	136.9 ± 3.6 (n = 66)	*n.s.*	*n.s.*	***	*n.s.*	*	*n.s.*

3.3.2 Flame Bowerbird

Sex-related and age-related variation

Morphological measurements of male and female Flame Bowerbirds (see Plate 26) are summarized in Table 3.6 for the northern taxon *aureus* and in Table 3.7 for the southern taxon *ardens*. Flame Bowerbirds show trends in sexual dimorphism in body size similar to Regent Bowerbirds. In both taxa of the Flame Bowerbird the traits tail length and bill width nostrils were significantly smaller in males than in females. In the taxon *ardens* the trait bill depth nostrils was also significantly smaller in males than in females. In both *aureus* and *ardens*, tail length measurements of immature males were intermediate between adult males and females.

Immature males show stages in the change to adult plumage resembling the moult sequence of male Regent Bowerbirds. However, in the Flame Bowerbird it is unknown how many annual moults are necessary to attain adult plumage because the age of the examined birds at the time when they were skinned is not known.

Several skins of the northern taxon *aureus* (e.g., immature males NRS 566728 and SMNS 10179, and female SMNS 8518b) showed pointed rectrices resembling the shape of pointed rectrices of first-year Regent Bowerbirds (see Fig. 3.2).

Table 3.6. Morphometric comparison of male and female northern Flame Bowerbirds, taxon *aureus*, for traits as defined in Table 3.1. Body mass is in g, all other measures are in mm.
Tab. 3.6. Morphometrischer Vergleich von männlichen und weiblichen Goldlaubenvögeln des nördlichen Taxons *aureus* für Merkmale wie in Tab. 3.1 definiert. Körpermasse ('body mass') in g, alle anderen Maße in mm.

Measure	Sample	Mean ± *s.d.*	*n*	*t*	*P*
Body mass	Male	157.1 ± 16.7	10	1.32	*n.s.*
	Female	170.3 ± 5.0	3		
Wing length	Male	140.1 ± 6.0	79	0.22	*n.s.*
	Female	139.7 ± 4.3	13		
Tail length	Male	85.3 ± 5.4	78	2.80	< 0.007**
	Female	89.7 ± 4.2	13		
Tail length	Ad. male	84.0 ± 4.8	45	4.13	< 0.001***
	Imm. male	88.9 ± 4.8	26	0.53	*n.s.*
	Female	89.7 ± 4.2	13		
Bill length	Male	22.7 ± 1.2	77	0.52	*n.s.*
	Female	22.9 ± 1.4	13		
Bill depth nostrils	Male	8.5 ± 0.6	48	0.15	*n.s.*
	Female	8.5 ± 0.7	10		
Bill width nostrils	Male	7.1 ± 0.4	59	4.17	< 0.001***
	Female	7.7 ± 0.6	10		

Table 3.7. Morphometric comparison of male and female southern Flame Bowerbirds, taxon *ardens*, for traits as defined in Table 3.1. All measures are in mm.
Tab. 3.7. Morphometrischer Vergleich von männlichen und weiblichen Goldlaubenvögeln des südlichen Taxons *ardens* für Merkmale wie in Tab. 3.1 definiert. Alle Maße in mm.

Measure	Sample	Mean ± *s.d.*	*n*	*t*	*P*
Wing length	Male	137.3 ± 2.3	18	1.26	*n.s.*
	Female	139.0 ± 1.0	3		
Tail length	Male	66.7 ± 4.9	17	3.02	< 0.008**
	Female	76.0 ± 5.6	3		
Tail length	Ad. male	65.6 ± 4.9	13	1.81	*n.s.*
	Imm. male	70.3 ± 2.7	4	1.83	*n.s.*
	Female	76.0 ± 5.6	3		
Bill length	Male	23.2 ± 0.5	15	1.43	*n.s.*
	Female	22.3 ± 1.0	3		
Bill depth nostrils	Male	7.6 ± 0.4	9	2.55	< 0.03*
	Female	8.3 ± 0.6	3		
Bill width nostrils	Male	6.8 ± 0.5	11	2.34	< 0.04*
	Female	7.5 ± 0.5	3		

Geographical variation

Morphological differences between the two taxa of the Flame Bowerbird are summarized in Table 3.8. Means for *aureus* were larger than means for *ardens* in all but one trait (bill length), though a level of significance was only attained in some measures. The traits tail length and bill depth nostrils were highly significantly larger in *aureus* than in *ardens* ($P < 0.001$), the trait wing length was also significantly larger in *aureus* ($P < 0.04$). A comparison of the localities where the specimens came from (see Table 3.9) reveals that the larger taxon *aureus* occurs in mountain ranges, whereas taxon *ardens* mainly occurs in lowlands and foothills.

The plumages of females and immature males of both taxa are similar (see BEEHLER et al. 1986; COATES 1990), whereas adult males are very distinct: those of *aureus* have the chin, throat and the sides of the head to around the eyes black (see Fig. 3.4), and those of *ardens* have the chin and throat yellow and the sides of the head orange (see Fig. 3.5). The bill of *aureus* is conspicuously black-tipped, whereas that of *ardens* is uniformly pale (Figs 3.4-3.5).

Table 3.8. Morphometric comparison of the two Flame Bowerbird taxa *aureus* and *ardens*. All measures are in mm.
Tab. 3.8. Morphometrischer Vergleich der beiden Goldlaubenvogel-Taxa *aureus* und *ardens*. Alle Maße in mm.

Measure	Sample	Mean ± *s.d.*	*n*	*t*	*P*
Wing length	*aureus*	140.3 ± 5.8	96	2.15	< 0.04*
	ardens	137.5 ± 2.2	21		
Wing length	*aur.*-male	140.1 ± 6.0	79	1.96	*n.s.*
	ard.-male	137.3 ± 2.3	18		
Wing length	*aur.*-female	139.7 ± 4.3	13	0.28	*n.s.*
	ard.-female	139.0 ± 1.0	3		
Tail length	*aureus*	86.0 ± 5.4	95	13.29	< 0.001***
	ardens	68.1 ± 5.9	20		
Tail length	*aur.*-male	85.3 ± 5.4	78	13.08	< 0.001***
	ard.-male	66.7 ± 4.9	17		
Tail length	*aur.*-female	89.7 ± 4.2	13	4.80	< 0.001***
	ard.-female	76.0 ± 5.6	3		
Bill length	*aureus*	22.8 ± 1.2	94	0.92	*n.s.*
	ardens	23.0 ± 1.0	18		
Bill depth nostrils	*aureus*	8.5 ± 0.6	58	4.15	< 0.001***
	ardens	7.7 ± 0.5	12		
Bill depth nostrils	*aur.*-male	8.5 ± 0.6	48	4.69	< 0.001***
	ard.-male	7.6 ± 0.4	9		
Bill depth nostrils	*aur.*-female	8.5 ± 0.7	10	0.55	*n.s.*
	ard.-female	8.3 ± 0.6	3		
Bill width nostrils	*aureus*	7.2 ± 0.4	69	1.90	*n.s.*
	ardens	6.9 ± 0.6	14		
Bill width nostrils	*aur.*-male	7.1 ± 0.4	59	2.68	< 0.01**
	ard.-male	6.8 ± 0.5	11		
Bill width nostrils	*aur.*-female	7.7 ± 0.6	10	0.44	*n.s.*
	ard.-female	7.5 ± 0.5	3		

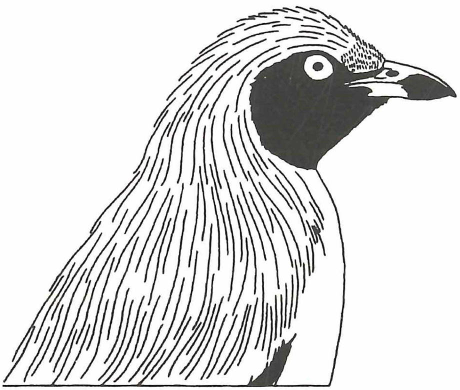

Figure 3.4. Portrait of an adult male northern Flame Bowerbird, taxon *aureus* (drawn after a painting by William T. Cooper in Cooper & Forshaw 1977).
Abb. 3.4. Porträt eines adulten männlichen Goldlaubenvogels des nördlichen Taxons *aureus* (gezeichnet nach einem Bild von William T. Cooper in Cooper & Forshaw 1977).

Table 3.9. Collecting and observation sites of the two Flame Bowerbird taxa *aureus* and *ardens*, their elevation above sea level and predominant types of vegetation.
Tab. 3.9. Fund- und Beobachtungsorte der beiden Goldlaubenvogel-Taxa *aureus* und *ardens*, ihre Höhe über dem Meeresspiegel und vorherrschende Vegetationstypen.

Taxon	Collecting and observation sites	Elevation and vegetation
aureus	Tamrau Mountains and Arfak Mountains on Doberai (Vogelkop) Peninsula, Fakfak Mountains on Onin (Fakfak) Peninsula, Wondiwoi Mountains on Wandammen Peninsula, Weyland Mountains and Idenburg slopes in western Central Dividing Range, Torricelli Mountains and Prince Alexander Mountains (with Mount Turu) in North Coastal Range	850-1400 m above sea level Lower montane rainforest (according to COATES 1990)
ardens	Wataikwa River, Noord River, Endrich River, Maro (Merauke) River near Merauke, upper Fly River near Kiunga, all in the southern lowlands	Up to 760 m above sea level Lowland rainforest and foothill monsoon forest (according to COATES 1990)

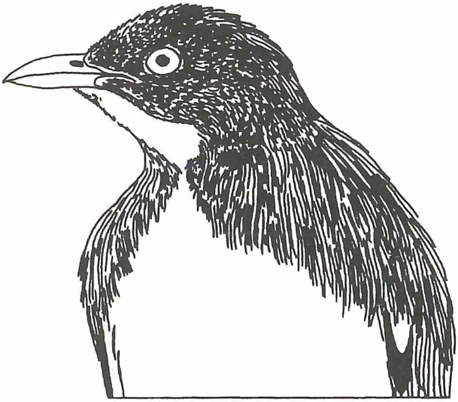

Figure 3.5. Portrait of an adult male southern Flame Bowerbird, taxon *ardens* (drawn after a painting by WILLIAM T. COOPER in COOPER & FORSHAW 1977).
Abb. 3.5. Porträt eines adulten männlichen Goldlaubenvogels des südlichen Taxons *ardens* (gezeichnet nach einem Bild von WILLIAM T. COOPER in COOPER & FORSHAW 1977).

3.3.3 Fire-maned Bowerbird

Morphological measurements of male and female Fire-maned Bowerbirds are summarized in Table 3.10. The tail length was significantly smaller in males than in females ($P < 0.004$). As in Regent and Flame Bowerbirds, tail length measurements of immature males were intermediate between adult males and females.

Means for the other two traits measured, body mass and wing length, were, however, larger in males than in females, though these differences were not significant. The small sample of body-mass measurements, obtained from the literature (GILLIARD & LECROY

1967), was taken in March and April (Gilliard 1969). Considering the breeding seasons of birds in Papua New Guinea (see Coates 1985), it is possible that the females were comparatively light because they had just finished breeding when they had been collected.

Table 3.10. Morphometric comparison of male and female Fire-maned Bowerbirds for traits as defined in Table 3.1. Body mass is in g, wing and tail lengths are in mm.
Tab. 3.10. Morphometrischer Vergleich von männlichen und weiblichen Rotscheitel-Laubenvögeln für Merkmale wie in Tab. 3.1 definiert. Körpermasse ('body mass') in g, Flügel- und Schwanzmaße ('wing and tail lengths') in mm.

Measure	Sample	Mean ± *s.d.*	*n*	*t*	*P*
Body mass	Male	177.8 ± 5.6	4	1.05	*n.s.*
	Female	172.6 ± 8.4	5		
Wing length	Male	138.7 ± 2.8	8	0.54	*n.s.*
	Female	137.7 ± 3.7	5		
Tail length	Male	81.3 ± 3.5	8	3.84	< 0.004**
	Female	89.7 ± 2.1	3		
Tail length	Ad. male	80.3 ± 2.9	5	1.07	*n.s.*
	Imm. male	83.0 ± 4.4	3	2.39	*n.s.*
	Female	89.7 ± 2.1	3		

3.4 Discussion

Sex- and age-related variation

The *Sericulus* species show a striking sexual dimorphism in plumage: adult males have contrasting, colourful plumages (see Figs 3.3-3.6 and Plates 25-26), whereas females have cryptic plumages (see illustrations in Cooper & Forshaw 1977 and Plates 19 and 26). The analysis of the morphometric measurements demonstrates that the *Sericulus* species are also sexually dimorphic in size. Male Regent Bowerbirds are highly significantly smaller than females in most traits analysed (Tables 3.2-3.3). Flame and Fire-maned Bowerbirds show similar trends (Tables 3.6, 3.7 and 3.10). This sexual size dimorphism, with females being larger than males, contrasts with the prediction of the sexual selection theory that males should be larger than females in bird species in which males compete for multiple mating opportunities (Darwin 1871; Payne 1984).

In field studies of behaviour and ecology of the Regent Bowerbird, morphometric measurements and knowledge of the moult sequence and plumage changes described above allow determination of the age and sex of most individuals. The traits with the most significant differences between sexes (bill width nostrils, bill depth nostrils, wing length, tail length and body mass) constitute the most useful criteria for distinguishing females and immature males.

Figure 3.6. Portrait of an adult male Fire-maned Bowerbird (drawn after a painting by PETER HAYMAN in EVERETT 1978).
Abb. 3.6. Porträt eines adulten männlichen Rotscheitel-Laubenvogels (gezeichnet nach einem Bild von PETER HAYMAN in EVERETT 1978).

Most results on sexual size dimorphism in the Regent Bowerbird confirm the findings of DISNEY & LANE (1971) and DISNEY (1971, 1974), who studied a small sample of 16 males and 22 females. However, their data came from the Iluka population of relatively small birds (see Tables 3.4-3.5). Most data presented in this study give larger measurements. DISNEY (1971, 1974) claimed that females usually have longer bills than males, which is refuted by the data in Table 3.2. The data in Table 3.3 indicate that wing lengths of adult and immature males overlap less often than suggested by DISNEY & LANE (1971).

Two of the three traits which did not show a significant difference between male and female Regent Bowerbirds are difficult to measure in museum specimens: head depth and tarsus plus middle toe length. Bill length measurements of males and females showed much overlap, but depth and width measurements of bills are considerably smaller in males than in females. Thus, the overall shape of bills is different: males have narrower bills, females broader and thicker ones. This difference could be indicative of intersexual differences in foraging (see SELANDER 1966, 1972).

The substantial sexual size dimorphism found in the Regent Bowerbird refutes PAYNE (1984), who called it the least size-dimorphic bowerbird species. Female Regent Bowerbirds are, on an average, 18.5 % heavier than males (115.8 g compared to 97.7 g, see Table 3.2). DONAGHEY (1981) found that male Satin Bowerbirds are 10.7 % heavier than females (216.7 g compared to 195.7 g) and males of the monogamous Green Catbird are 5.7 % heavier than females (213.5 g compared to 202.0 g). This shows that PAYNE's method of comparing ranges of measurements obtained from the literature was clearly inadequate for studying sexual size dimorphism in bowerbirds.

PAYNE (1984) did, however, find a similarly-reversed sexual size dimorphism (with females being larger than males) in some other bird species in which individual males mate with several females: for example, in some species of bustards (Otididae), hummingbirds (Trochilidae) and manakins. Those species with reversed size dimorphism are the smallest in the bird families concerned (PAYNE l.c.). Likewise, the Regent Bowerbird with its reversed size dimorphism is one of the smallest bowerbird species. PAYNE (l.c.) suggested that the form of the male display may be one factor accounting for reversed size dimorphism, as did SNOW (1982) and HÖGLUND (1989). The sexual selection theory would predict that aggressive encounters between males are less important in species with reversed size dimorphism, such as the Regent Bowerbird (see Chapter 7), than in species with large males (DARWIN 1871; KREBS & DAVIES 1987).

Morphometric data of Flame and Fire-maned Bowerbirds show statistically significant intersexual differences in only few traits (tail length, bill depth nostrils and bill width nostrils). This is probably due to insufficient sample sizes, as whether or not a particular measure attains a level of statistical significance is very much a function of sample size (see YOM-TOV & NIX 1986).

The plumages of all adult *Sericulus* males are combinations of the colours golden-yellow, orange-red and velvety-black, the most colourful feathers being in the crown, nape and wings (see Figs 3.3-3.6 and Plates 25-26). It may be expected that these plumage parts feature prominently in their sexual displays. Passerine bird species with similar plumage patterns evolved in closed forests world-wide and provide an example of convergent evolution (BEEHLER 1982) that may be related to similar light environments (J.A. ENDLER & D.N. JONES in litt.). For example, males of several oriole species (Oriolidae) have plumage colours similar to *Sericulus* species. Similarities with some Neotropical closed forest-dwelling passerines are striking: the wing colouring of the Black and Gold Cotinga *Tijuca atra* resembles the wings of male Regent and Fire-maned Bowerbirds, and the head and underparts colouration of the Wire-tailed Manakin *Pipra filicauda* resembles the male southern Flame Bowerbird (taxon *ardens*). The contrasting plumages of these birds can be very conspicuous during sexual displays, but yet are surprisingly cryptic in the contrasting shadows of the forest canopy.

The results on moult sequence and plumage changes in the Regent Bowerbird resemble VELLENGA's (1980a) findings on the Satin Bowerbird. In both species immature males are female-plumaged and usually obtain full adult plumage in their seventh year, with the sixth annual moult. As the male is the larger sex in Satin Bowerbirds, remiges and rectrices of immature males are longer than those of females. In contrast, wing and tail lengths of immature males of the Regent Bowerbird are smaller than those of females and larger than those of adult males (Table 3.3). The same proportions apply to tail lengths of congeneric Flame and Fire-maned Bowerbirds (Tables 3.6, 3.7 and 3.10). Morphometric measurements of immature males intermediate between females and adult males have also been found in other passerine bird species in which the female is the larger sex: for example, in the Fan-tailed Berrypecker *Melanocharis versteri* (DIAMOND 1972) and in cotingas of the genus *Phoenicircus* (SNOW 1982).

The wing design of a bird is correlated with its behaviour and ecology (RAYNER 1988). MAYR & JENNINGS (1952) suggested that the wing-shape modification of male Regent Bowerbirds, adult males having shorter wings than immature males, is correlated with the courtship display of the adult male. A reduction in wing length and wing span reduces the aspect ratio of wings (BROOKE & BIRKHEAD 1991), a parameter quantifying the wing dimensions in studies of bird flight (aspect ratio = wing span squared divided by wing area). This reduction in aspect ratio leads to poor aerodynamic performance and increases mechanical energy costs in flight, but improves flexibility in mode of flight and manoeuvrability (see Fig. 3.7). These advantages of a low aspect ratio should outweigh the metabolic costs, as male Regent Bowerbirds are not known to migrate long distances (see Chapter 5), but live and display in densely-vegetated habitat, cluttered with obstacles such as lianas and thorny shrubs (see Chapters 6 and 7). A similar reduction in the aspect ratio is shown by adult male red cotingas *Phoenicircus* spp. and manakins *Pipra* spp., passerines from Neotropical forests. SNOW (1982) suggested that the wing design in these species is an adaptation to displays which involve rapid aerial manoeuvres.

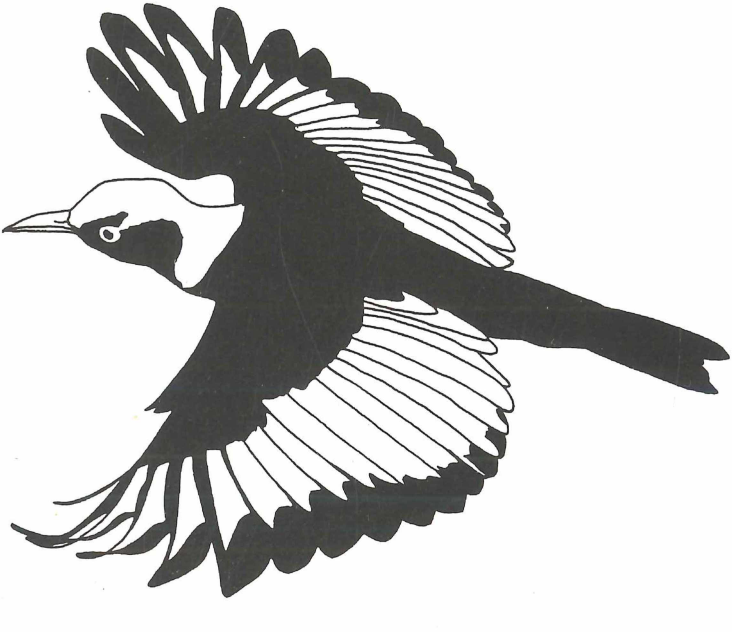

Figure 3.7. Adult male Regent Bowerbird in flapping flight (drawn after a photograph by LEN ROBINSON). The short and rounded wings cause low aspect ratio (= wing span squared divided by wing area), poor aerodynamic performance and high metabolic costs, but make very good manoeuvrability in dense rainforest habitat possible.

Abb. 3.7. Adulter männlicher Gelbnacken-Laubenvogel im Schlagflug (gezeichnet nach einer Fotografie von LEN ROBINSON). Die kurzen und abgerundeten Flügel bewirken eine geringe Flügelstreckung (= Quadrat der Spannweite dividiert durch die Flügelfläche), geringe aerodynamische Leistungen und hohe Stoffwechselkosten, ermöglichen aber sehr gute Manövrierfähigkeit in dichtem Regenwaldhabitat.

Zoogeography, geographical variation and taxonomy

The bright plumage of adult males of the *Sericulus* species confused early taxonomists, who described them variously as rollers (Coraciidae), honeyeaters (Meliphagidae), orioles and birds of paradise (MATHEWS 1927). After the discovery of bowers built by *Sericulus* males, IREDALE (1948) still regarded the genus as a taxon of anomalous bowerbirds and gave it the status of a separate subfamily Sericulinae. BOCK (1963) and SCHODDE (1976) regarded *Sericulus* as a taxon closely related to the birds of paradise subfamily Cnemophilinae, bridging the two Australo-Papuan families. Studies of DNA data (SIBLEY & AHLQUIST 1985, 1990; cf. CHRISTIDIS & SCHODDE 1991, 1992) have, however, shown that bowerbirds are not closely related to birds of paradise and that lyrebirds (Menuridae) and scrub-birds (Atrichornithidae) represent the sister group of the bowerbird family. Any similarities in the biology of bowerbirds, including the genus *Sericulus*, and birds of paradise are thus the result of convergent evolution rather than close phylogenetic relationship.

The geographical distribution of the genus *Sericulus* (see Fig. 3.1) shows a patchy, relictual range (DIAMOND 1969; SCHODDE 1976; PRATT 1982). A similar pattern of distribution, involving mountains and lowlands of New Guinea and separated areas of rainforest (closed forest) in eastern Australia, is shared with some other taxa, such as the Logrunner and the King-Parrot *Alisterus* spp. superspecies complex (see BLAKERS et al. 1984; COATES 1985, 1990). This distributional pattern is indicative of taxa which have invaded Australia from the mountains of New Guinea or vice versa (DIAMOND 1969).

Regent Bowerbird populations show some significant size differences (Table 3.5). Most of these conform with BERGMANN's (1847) zoogeographical rule, just as the size differences in many other Australian bird species do, such as Superb Fairy-wren *Malurus cyaneus* and Brown Thornbill *Acanthiza pusilla* (ROGERS et al. 1986, 1990). Among bowerbirds, the aptly-named northern subspecies of the Satin Bowerbird *P. v. minor* is smaller than the southern subspecies *P. v. violaceus* (GILLIARD 1969). However, not all species and not all populations follow the general pattern of being smaller in the warmer part of their range: for example, Tasmanian Grey Fantails *Rhipidura fuliginosa* and Eastern Spinebills *Acanthorhynchus tenuirostris* are smaller than Victorian ones (ROGERS et al. 1986, 1990). In the Regent Bowerbird, individuals from the southernmost mountain ranges (area F in Table 3.5) were relatively small. The sample from this area consisted of a small number of old museum specimens. Besides this deficiency of the sample, knowledge of differences in the biology of populations (e.g. types of movements) is required for a complete understanding of size differences between them.

The examination of Regent Bowerbird skins in zoological collections showed no geographical plumage variation in females and immature males, but a brighter colouring of adult males from the northern part of the range. The latter could provide adequate reason for recognizing the subspecies *S. c. rothschildi*, though this taxon does not show a consistent size difference to *S. c. chrysocephalus*. The range of *rothschildi* extends from the Clarke Range in the north to approximately the McPherson Range in the south. The recognition of the two subspecies should be adjourned until the limits of distribution and the characters defining each form are better known.

The two distinct taxa of the Flame Bowerbird were initially regarded as separate species (VAN OORT 1909; MATHEWS 1927; IREDALE 1948). Since specimens of *ardens* showing some evidence of gene flow with *aureus* in their plumage colouration were collected at the Wataikwa River in south-western New Guinea (OGILVIE-GRANT 1915), the two taxa were considered conspecific (RAND & GILLIARD 1967; GILLIARD 1969; WOLTERS 1975-1982; COOPER & FORSHAW 1977; HOWARD & MOORE 1980; WALTERS 1980; BEEHLER & FINCH 1985; BEEHLER et al. 1986; COATES 1990; PERRINS 1990; SIBLEY & MONROE 1990). The latter view ignores the fact that the two taxa are not only different in plumage and bill colouration but also in morphology: *ardens* has a proportionately shorter tail, shorter wings, and a much narrower bill than *aureus* (Table 3.8). OGILVIE-GRANT (1915), in his original description of the Wataikwa River specimens, regarded *aureus* and *ardens* as distinct species, but has often been misquoted (e.g. COATES 1990). The two taxa represent two distinct, diagnosable, monophyletic clusters of individuals, almost completely isolated by the central mountain range of New Guinea. When using the phylogenetic species concept (see MCKITRICK & ZINK 1988; CRACRAFT 1992), *aureus* and *ardens* would clearly be species.

Even when using the traditional biological species concept (see MAYR 1942), the possibility of hybridization does not necessarily imply that two taxa are subspecies of one species. Some Wataikwa River specimens might indeed be hybrids (e.g. BMNH 1916.5.30.1017, which has a tail length intermediate between *aureus* and *ardens*); this locality is close to the narrowest part of the central mountain range of New Guinea. But natural interspecific hybridization has been documented in a number of bird species, such as some grouse (JOHNSGARD 1983) and birds of paradise (STRESEMANN 1930; FULLER 1979, 1995; FRITH & BEEHLER 1998). For example, the birds of paradise Ribbon-tailed Astrapia *Astrapia mayeri* and Stephanie's Astrapia *A. stephaniae* of New Guinea regularly produce hybrids where they co-occur (FULLER 1979; COATES 1990; BEEHLER 1991; FRITH & BEEHLER 1998), but they are recognized as two species because both represent monophyletic clusters of individuals with distinct differences in morphology and plumage. A similar treatment seems appropriate for Flame Bowerbirds (see Appendix 6).

The Fire-maned Bowerbird has a very restricted range, being confined to a narrow altitudinal band in the isolated Adelbert Mountains of Papua New Guinea (BEEHLER et al. 1986; COLLAR & ANDREW 1988; COATES 1990). Numerically it may be the rarest bird species of New Guinea, and BirdLife International listed its status as 'vulnerable' (BEEHLER 1985b; MOUNTFORT & ARLOTT 1988; COLLAR et al. 1994). Due to the limited range, geographical variation is unlikely in this species.

A comparison of the *Sericulus* species from New Guinea with the Australian Regent Bowerbird shows that all species in this genus are generally similar in their pattern of sexual dimorphism. The similarity of all *Sericulus* species in their morphology and plumage does not support the view that the sympatry of the closely-related Regent and Satin Bowerbirds has been an important factor in the evolution of the Regent Bowerbird.

4 Food, Foraging and Dietary Relationships

4.1 Introduction

The vast majority of the over 5000 species in the large avian order Passeriformes is territorial and has a monogamous mating system (ORING 1982; BEZZEL & PRINZINGER 1990; BROOKE & BIRKHEAD 1991). Most of the non-monogamous species are frugivores, species predominantly feeding on fruit. Therefore, a relationship between frugivory and polygamy has been hypothesized (SNOW 1962a,b, 1971, 1980; WILLIS 1979; BEEHLER 1983a; BROOKE & BIRKHEAD 1991).

The use of fruit as food resource has a number of advantages: fruit is often very nutritious (rich especially in carbohydrates), relatively simple to harvest and locally abundant (SNOW 1971; LILL 1976; BEEHLER 1983a; BEGON et al. 1986; SNOW & SNOW 1988). Fruit is particularly abundant in tropical forest ecosystems, where most non-monogamous passerines occur. Males of these tropical frugivores can quickly satisfy their daily energy requirements and invest the remaining daylight hours in other activities, such as advertising themselves as mates through courtship displays and calls (FOSTER 1977; BEEHLER 1983a).

The correlation between diet and mating system has been studied in several families of passerine birds. In the Neotropical cotingas, manakins and tyrant flycatchers (Tyrannidae), most monogamous species are predominantly insectivorous, whereas most non-monogamous species are frugivorous (e.g. D.W. SNOW 1962a,b, 1973, 1980, 1982; B.K. SNOW 1970, 1972, 1977; LILL 1974a,b, 1975, 1976; WILLIS et al. 1978; SNOW & SNOW 1979; WILLIS 1979).

In birds of paradise, monogamous species are specialized frugivores, whereas most non-monogamous species are more generalized frugivores, with a large percentage of complex, capsular fruits in their diets. The few bird of paradise species with a large percentage of arthropods in their diets are also non-monogamous, in contrast to the Neotropical families mentioned above. Thus, the correlation between diet and mating system is more complex than frequently suggested, though frugivory is still believed to have been of importance in the evolution of polygamy in birds of paradise (BEEHLER 1983a,b, 1985a, 1987, 1988, 1989, 1991; BEEHLER & PRUETT-JONES 1983; FRITH & FRITH 1992; FRITH & BEEHLER 1998).

Catbirds and bowerbirds combine fruit, invertebrates and small vertebrates in their diet (FORD 1989; BARKER & VESTJENS 1990). DONAGHEY (1981) compared foraging and reproductive biology of two species of the bowerbird family, Green Catbird and Satin Bowerbird, both primarily frugivorous. A large percentage of the Green Catbird diet consisted of figs of the species *Ficus watkinsiana*, whereas no single item predominated in the diet of Satin Bowerbirds. *Ficus watkinsiana* trees were found to be randomly spatially dispersed and the availability of their figs was temporally predictable. In contrast, food plants of Satin Bowerbirds were more unpredictable in their spatio-temporal availability. DONAGHEY (l.c.) concluded that these differences in the availability of food sources may cause differences in their economical defendability, thus promoting differences in the reproductive biology of the two species. Green Catbirds are monogamous, territorial and provide biparental brood care, whereas the non-monogamous Satin Bowerbirds have overlapping home ranges and provide uniparental female brood care.

The diet of the Regent Bowerbird is poorly known. BARKER & VESTJENS (1990) list eight items of plant material and four items of animal material which Regent Bowerbirds have been observed to feed on. This short list is obviously incomplete.

It is the aim of this chapter to provide the first detailed study of food and foraging of the Regent Bowerbird. The foraging of Regent Bowerbirds, in particular fruit-eating, shall be compared with that of two sympatric species of the bowerbird family, Green Catbird and Satin Bowerbird, and the relationship between diet and mating organization shall be discussed. If frugivory has been important in the evolution of non-monogamous mating systems in the bowerbird family, it may be expected that the closely-related Regent and Satin Bowerbirds should have more dietary overlap than either one of the two bower-building species should have with the monogamous Green Catbird.

4.2 Methods

The method most often used in studies addressing the relationship between ecology and behaviour is the comparative approach (see references in EMLEN & ORING 1977; WITTENBERGER 1979; ORING 1982; BEEHLER 1987). To allow a comparison of food and foraging of Regent Bowerbirds with that of other species of the bowerbird family the sampling method of DONAGHEY (1981), who studied foods of Green Catbirds and Satin Bowerbirds in the Tooloom Scrub rainforest in north-eastern New South Wales, was adopted.

Most data were collected by means of opportunistic direct observations of foraging birds during regular searches for bowers throughout the Sarabah Range study area and in adjacent areas of Lamington National Park (see Chapter 6). Outside mating and breeding seasons, from March to July, observations were made along Lamington National Park Road only, and records from this time of the year may be biased towards the top of the ridge and the forest edge (see Chapter 2). Additional data were collected by examination of faecal samples collected during banding of birds and from immediately about a pool near the banding site, which was frequently visited by catbirds and bowerbirds for drinking and bathing.

The unit of measure was the 'feeding record'. An observation of a bird feeding on a food item constituted one feeding record. To limit bias, maximum numbers of records per day were limited to five records per individual and ten records per foraging flock. Two different individuals observed feeding on the same food item counted as two records, whereas the same individual repeatedly observed consuming the same type of dietary item on one day counted as only one record. However, an observation of an individual consuming both fruit and leaves of one plant species on one day was scored as two records. An individual observed repeatedly feeding on animals was scored successively up to five records per day, although it was often impossible to ascertain whether the same or a different species of small arthropod was consumed.

Plant species were identified using STANLEY & ROSS (1983, 1986, 1989), WILLIAMS & HARDEN (1984) and WILLIAMS et al. (1984). Nomenclature of plant species and morphology follows STANLEY & ROSS (1983, 1986, 1989). Observations at introduced plants were only given scores when they concerned naturalized species. In addition to the identity of the food items consumed, notes on the foraging method were made. Much foraging took place in the canopy, which often made it impossible to ascertain whether a 'brown' Regent Bowerbird was a female or an immature male (see Chapter 3); therefore, intersexual differences in foraging were not analysed.

In his study of the foraging of Green Catbirds and Satin Bowerbirds, DONAGHEY (1981) used the total number of feeding records to calculate the percentage of records for each dietary component in the annual diet as an index for the importance of a dietary component. This method ignores differences between monthly numbers of feeding records. In both DONAGHEY's study and this study, more feeding records were gathered in summer than in winter months. Therefore, it is more appropriate to calculate monthly percentages for each dietary component, to add up the monthly percentages, and to take the twelfth of this sum as an index for the importance of a dietary component in the annual diet.

A comparison of the frugivorous habits of Regent Bowerbirds in the Sarabah Range with DONAGHEY's (1981) data of Green Catbirds and Satin Bowerbirds in the Tooloom Scrub is limited in value by differences in floristic composition between the two areas. To enable a discussion on the relationship between diet and mating organization in the three species of the bowerbird family, data of fruit-eating by Green Catbirds and Satin Bowerbirds were also gathered in the Sarabah Range, in addition to the Regent Bowerbird feeding records. In order to analyse dietary relationships of the three species, the breadth and overlap in their frugivorous diet were calculated.

Diet niche breadths, B, were calculated using the normalized measure of LEVINS (1968):

$$B = \frac{1}{R\sum_{i=1}^{n} p_i^2}$$

where p_i is the proportion of food resource i in the diet of a species, and R is the total number of different food resource categories available, for example, the number of species of fruit. Niche breadth B varies from $1/R$ (only one category of food resource taken) to 1.0 (all available food categories taken equally).

Dietary niche overlaps, O, were calculated using the symmetrical measure of PIANKA (1973, 1974):

$$O_{jk} = O_{kj} = \frac{\sum_{i=1}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i=1}^{n} p_{ij}^2 \sum_{i=1}^{n} p_{ik}^2}}$$

where p_{ij} and p_{ik} represent the proportions of food resource i in the diets of species j and k respectively. Niche overlap O varies from 0 (no overlap in the food categories consumed by species pair j and k) to 1.0 (complete overlap).

Following BEEHLER (1983a), fruits were classified into three morphological categories: figs, drupes/berries and capsules. Figs, the fruits from plants of the genus *Ficus*, are aggregates of numerous small achenes, enclosed in an enlarged, fleshy receptacle. Simple, compound or aggregate indehiscent fruits with seeds surrounded by a fleshy pericarp were assigned to the class drupe/berry. Fruits with seeds enclosed in an edible part, such as an aril or testa, within an inedible, dehiscent fruit were assigned to the class capsule.

4.3 Results

4.3.1 Food and foraging of the Regent Bowerbird

Composition of the diet

Feeding records of Regent Bowerbirds are summarized in Table 4.1. Regent Bowerbirds have a varied, though predominantly frugivorous diet. A total of 1193 feeding records was gathered, 854 of which were records of fruit-eating, 172 were feeding records on flowers, 23 were records of leaf-eating, and 144 were feeding records on animal foods (feeding records on fruit, flowers, leaves and animal foods are summarized at the end of each of these dietary components in Table 4.1).

Fruit-eating predominated in most months and was supplemented by nectarivorous foraging in spring, by insectivorous foraging in spring and summer and by folivorous foraging in winter (see Fig. 4.1). The proportion of records of feeding on fruit, flowers, leaves and animal foods differed strongly between spring/summer (September to February, mating and breeding seasons) and the rest of the year ($\chi^2 = 147.0$, *d.f.* = 3, $P < 0.00001$).

Table 4.1. Foods of Regent Bowerbirds. Number of feeding records (upper lines) and percentage (lower lines) in monthly and annual diet (mean of monthly percentages) for each food item. * = introduced species.

Tab. 4.1. Nahrung von Gelbnacken-Laubenvögeln. Anzahl beobachteter Nahrungsaufnahmen (obere Zeilen) und prozentualer Anteil aller Nahrungsobjekte (untere Zeilen) im Nahrungsspektrum pro Monat und im Jahr (Mittelwert der prozentualen Anteile pro Monat). * = eingeführte Art.

Food item	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Total
Fruit:													
Acacia	0	0	0	0	0	1	0	0	0	0	0	0	1
maidenii	0	0	0	0	0	1.0	0	0	0	0	0	0	0.1
Acmena	0	1	0	0	0	0	0	0	0	0	0	0	1
brachyandra	0	2.2	0	0	0	0	0	0	0	0	0	0	0.2
Acmena	2	0	0	0	0	0	0	0	0	0	0	0	2
smithii	7.7	0	0	0	0	0	0	0	0	0	0	0	0.6
Acronychia	0	1	1	2	6	0	0	0	0	0	0	0	10
oblongifolia	0	2.2	1.5	0.8	4.0	0	0	0	0	0	0	0	0.7
Akania	0	0	0	0	0	0	0	0	0	4	0	0	4
lucens	0	0	0	0	0	0	0	0	0	3.4	0	0	0.3
Alangium	0	0	0	0	0	0	6	0	0	0	0	0	6
villosum	0	0	0	0	0	0	5.9	0	0	0	0	0	0.5
Alphitonia	0	0	0	0	0	12	14	19	0	0	0	0	45
excelsa	0	0	0	0	0	11.7	13.9	15.2	0	0	0	0	3.4
Amylotheca	0	0	0	0	0	0	0	0	2	0	0	0	2
dictyophleba	0	0	0	0	0	0	0	0	1.9	0	0	0	0.2
Brachychiton	0	1	5	0	0	0	0	0	0	0	0	0	6
acerifolius	0	2.2	7.4	0	0	0	0	0	0	0	0	0	0.8
Carissa	0	0	0	0	0	0	1	0	0	0	0	0	1
ovata	0	0	0	0	0	0	1.0	0	0	0	0	0	0.1
Cayratia	0	0	0	0	0	0	0	0	0	2	0	0	2
clematidea	0	0	0	0	0	0	0	0	0	1.7	0	0	0.1
Cayratia	0	0	0	0	0	0	0	0	0	3	0	0	3
eurynema	0	0	0	0	0	0	0	0	0	2.5	0	0	0.2
Cephalaralia	0	0	0	0	0	0	0	0	0	0	0	1	1
cephalobotrys	0	0	0	0	0	0	0	0	0	0	0	2.1	0.2
Cissus	0	0	0	0	0	0	0	1	1	3	0	0	5
antarctica	0	0	0	0	0	0	0	0.8	0.9	2.5	0	0	0.4
Citrus	0	1	0	0	0	0	0	0	0	0	0	0	1
*limon**	0	2.2	0	0	0	0	0	0	0	0	0	0	0.2
Cordyline	0	0	0	0	0	0	2	0	0	0	0	0	2
petiolaris	0	0	0	0	0	0	2.0	0	0	0	0	0	0.2
Cordyline	0	0	0	0	0	0	0	0	1	0	0	0	1
rubra	0	0	0	0	0	0	0	0	0.9	0	0	0	0.1
Cryptocarya	0	0	0	0	0	1	0	1	0	0	0	0	2
bidwillii	0	0	0	0	0	1.0	0	0.8	0	0	0	0	0.1

Table 4.1 (continued). – Tab. 4.1 (Fortsetzung).

Food item	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Total
Fruit (continued):													
Cudrania	0	0	0	0	3	4	1	2	0	0	0	0	10
cochinchinensis	0	0	0	0	2.0	3.9	1.0	1.6	0	0	0	0	0.7
Dendrocnide	11	0	0	0	0	0	0	0	0	0	7	29	47
excelsa	42.3	0	0	0	0	0	0	0	0	0	12.3	60.4	9.6
Dianella	0	0	0	0	1	2	1	0	0	1	0	0	5
caerulea	0	0	0	0	0.7	1.9	1.0	0	0	0.8	0	0	0.4
Diospyros	0	0	0	0	0	0	0	0	4	0	0	0	4
ferrea	0	0	0	0	0	0	0	0	3.7	0	0	0	0.3
Diospyros	0	1	0	0	0	1	3	7	6	0	0	0	18
pentamera	0	2.2	0	0	0	1.0	3.0	5.6	5.6	0	0	0	1.4
Diplocyclos	0	0	0	0	0	0	0	0	0	0	0	5	5
palmatus	0	0	0	0	0	0	0	0	0	0	0	10.4	0.9
Diploglottis	0	0	0	0	1	32	3	6	0	0	0	0	42
cunninghamii	0	0	0	0	0.7	31.1	3.0	4.8	0	0	0	0	3.3
Duchesnea	0	0	0	0	0	1	2	1	0	0	0	0	4
*indica**	0	0	0	0	0	1.0	2.0	0.8	0	0	0	0	0.3
Dysoxylum	0	0	0	0	0	4	0	0	0	0	0	0	4
rufum	0	0	0	0	0	3.9	0	0	0	0	0	0	0.3
Ehretia	0	0	0	0	0	0	0	0	3	0	0	0	3
acuminata	0	0	0	0	0	0	0	0	2.8	0	0	0	0.2
Elaeocarpus	0	0	0	0	0	0	0	19	44	32	18	0	113
obovatus	0	0	0	0	0	0	0	15.2	41.1	26.9	31.6	0	9.6
Elattostachys	0	0	0	0	0	0	0	0	0	2	2	0	4
xylocarpa	0	0	0	0	0	0	0	0	0	1.7	3.5	0	0.4
Ficus	0	0	0	0	2	0	0	0	0	0	0	0	2
coronata	0	0	0	0	1.3	0	0	0	0	0	0	0	0.1
Ficus	0	0	0	2	0	0	0	0	0	0	0	0	2
fraseri	0	0	0	0.8	0	0	0	0	0	0	0	0	0.1
Ficus	0	0	6	6	0	0	0	6	0	0	0	0	18
macrophylla	0	0	8.8	2.4	0	0	0	4.8	0	0	0	0	1.3
Ficus	0	0	0	3	4	0	0	0	0	0	0	0	7
obliqua	0	0	0	1.2	2.7	0	0	0	0	0	0	0	0.3
Ficus	0	0	1	6	19	13	5	0	0	0	0	0	44
platypoda	0	0	1.5	2.4	12.8	12.6	5.0	0	0	0	0	0	2.9
Ficus	6	5	6	0	13	6	36	0	7	0	0	0	79
superba	23.1	11.1	8.8	0	8.7	5.8	35.6	0	6.5	0	0	0	8.3
Ficus	0	0	0	0	0	0	0	4	3	5	0	0	12
watkinsiana	0	0	0	0	0	0	0	3.2	2.8	4.2	0	0	0.8
Jagera	0	0	9	4	2	0	0	0	0	0	0	0	15
pseudorhus	0	0	13.2	1.6	1.3	0	0	0	0	0	0	0	1.4
Jasminum	0	0	0	1	0	0	0	0	0	0	0	0	1
dallachii	0	0	0	0.4	0	0	0	0	0	0	0	0	<0.1

Table 4.1 (continued). – Tab. 4.1 (Fortsetzung).

Food item	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Total
Fruit (continued):													
Lantana	0	0	0	0	0	0	1	0	0	0	0	0	1
*camara**	0	0	0	0	0	0	1.0	0	0	0	0	0	0.1
Litsea	0	0	0	0	0	0	0	1	0	0	0	0	1
reticulata	0	0	0	0	0	0	0	0.8	0	0	0	0	0.1
Melia	0	0	0	0	0	0	0	1	0	0	0	2	3
azedarach	0	0	0	0	0	0	0	0.8	0	0	0	4.2	0.4
Mischocarpus	0	0	0	0	0	0	0	0	0	5	0	0	5
anodontus	0	0	0	0	0	0	0	0	0	4.2	0	0	0.4
Morinda	0	0	0	0	0	0	0	2	0	0	0	0	2
jasminoides	0	0	0	0	0	0	0	1.6	0	0	0	0	0.1
Olea	0	12	31	41	16	0	0	0	0	0	0	0	100
paniculata	0	26.7	45.6	16.7	10.7	0	0	0	0	0	0	0	8.3
Phytolacca	0	0	0	0	0	0	0	0	0	1	1	1	3
*octandra**	0	0	0	0	0	0	0	0	0	0.8	1.8	2.1	0.4
Piper novae-	0	0	0	0	0	0	6	13	0	0	0	0	19
hollandiae	0	0	0	0	0	0	5.9	10.4	0	0	0	0	1.4
Pittosporum	0	0	0	0	0	0	0	1	2	8	15	1	27
undulatum	0	0	0	0	0	0	0	0.8	1.9	6.7	26.3	2.1	3.1
Polyscias	0	5	0	0	0	0	0	0	0	21	11	6	43
elegans	0	11.1	0	0	0	0	0	0	0	17.6	19.3	12.5	5.0
Premna	0	8	0	0	0	0	0	0	0	0	0	0	8
lignum-vitae	0	17.8	0	0	0	0	0	0	0	0	0	0	1.5
Rhodamnia	0	0	0	0	0	0	0	0	11	11	0	0	22
argentea	0	0	0	0	0	0	0	0	10.3	9.2	0	0	1.6
Rubus	0	0	0	3	0	0	1	0	0	0	0	1	5
moluccanus	0	0	0	1.2	0	0	1.0	0	0	0	0	2.1	0.4
Rubus	0	3	0	0	1	0	0	0	0	0	0	0	4
rosifolius	0	6.7	0	0	0.7	0	0	0	0	0	0	0	0.6
Sarcopteryx	0	0	0	0	0	5	0	0	0	0	0	0	5
stipata	0	0	0	0	0	4.9	0	0	0	0	0	0	0.4
Scolopia	0	0	0	0	0	0	0	5	4	0	0	0	9
braunii	0	0	0	0	0	0	0	4.0	3.7	0	0	0	0.6
Solanum	0	4	0	0	0	0	8	0	0	1	0	0	13
aviculare	0	8.9	0	0	0	0	7.9	0	0	0.8	0	0	1.5
Solanum	0	0	0	0	6	4	2	0	0	5	0	0	17
*mauritianum**	0	0	0	0	4.0	3.9	2.0	0	0	4.2	0	0	1.2
Solanum	0	0	0	0	0	1	1	0	0	1	0	0	3
*nigrum**	0	0	0	0	0	1.0	1.0	0	0	0.8	0	0	0.2
Symplocos	0	0	0	0	0	0	0	12	6	0	0	0	18
thwaitesii	0	0	0	0	0	0	0	9.6	5.6	0	0	0	1.3
Synoum	0	0	0	0	0	0	0	0	0	0	2	2	4
glandulosum	0	0	0	0	0	0	0	0	0	0	3.5	4.2	0.6

Table 4.1 (continued). – Tab. 4.1 (Fortsetzung).

Food item	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Total
Fruit (continued):													
Tetrastigma	0	0	0	0	0	0	0	0	3	4	0	0	7
nitens	0	0	0	0	0	0	0	0	2.8	3.4	0	0	0.5
Trochocarpa	0	0	0	1	0	0	0	0	0	0	0	0	1
laurina	0	0	0	0.4	0	0	0	0	0	0	0	0	<0.1
Total fruit	19	42	59	69	74	87	93	101	97	109	56	48	854
Percentage	73.1	93.3	86.8	28.2	49.7	84.5	92.1	80.8	90.7	91.6	98.2	100	80.7
Flowers:													
Acacia	0	0	0	0	0	0	1	0	0	0	0	0	1
melanoxylon	0	0	0	0	0	0	1.0	0	0	0	0	0	0.1
Aphananthe	0	0	0	0	0	1	0	0	0	0	0	0	1
philippinensis	0	0	0	0	0	1.0	0	0	0	0	0	0	0.1
Brachychiton	0	0	0	0	3	7	0	0	0	0	0	0	10
acerifolius	0	0	0	0	2.0	6.8	0	0	0	0	0	0	0.7
Capparis	0	0	0	0	0	0	1	0	0	0	0	0	1
arborea	0	0	0	0	0	0	1.0	0	0	0	0	0	0.1
Callistemon	0	0	0	5	0	0	0	0	0	0	0	0	5
viminalis	0	0	0	2.0	0	0	0	0	0	0	0	0	0.2
Cordyline	0	0	0	0	1	0	0	0	0	0	0	0	1
rubra	0	0	0	0	0.7	0	0	0	0	0	0	0	0.1
Grevillea	0	0	5	101	44	0	0	0	0	0	0	0	150
robusta	0	0	7.4	41.2	29.5	0	0	0	0	0	0	0	6.5
Lantana	0	1	0	1	0	0	0	0	0	0	0	0	2
*camara**	0	2.2	0	0.4	0	0	0	0	0	0	0	0	0.2
Melia	0	0	0	0	1	0	0	0	0	0	0	0	1
azedarach	0	0	0	0	0.7	0	0	0	0	0	0	0	0.1
Total flowers	0	1	5	107	49	8	2	0	0	0	0	0	172
Percentage	0	2.2	7.4	43.7	32.9	7.8	2.0	0	0	0	0	0	8.0
Leaves:													
Anagallis	0	0	1	0	0	0	0	0	0	0	0	0	1
*arvensis**	0	0	1.5	0	0	0	0	0	0	0	0	0	0.1
Passiflora	6	2	1	1	0	0	1	0	0	0	1	0	12
*subpeltata**	23.1	4.4	1.5	0.4	0	0	1.0	0	0	0	1.8	0	2.7
Pittosporum	0	0	2	6	1	0	0	0	0	0	0	0	9
undulatum	0	0	2.9	2.4	0.7	0	0	0	0	0	0	0	0.5
Solanum	1	0	0	0	0	0	0	0	0	0	0	0	1
*mauritianum**	3.8	0	0	0	0	0	0	0	0	0	0	0	0.3
Total leaves	7	2	4	7	1	0	1	0	0	0	1	0	23
Percentage	26.9	4.4	5.9	2.9	0.7	0	1.0	0	0	0	1.8	0	3.6
Total animals	0	0	0	62	25	8	5	24	10	10	0	0	144
Percentage	0	0	0	25.3	16.8	7.8	5.0	19.2	9.3	8.4	0	0	7.6
Total feeding records:	26	45	68	245	149	103	101	125	107	119	57	48	1193

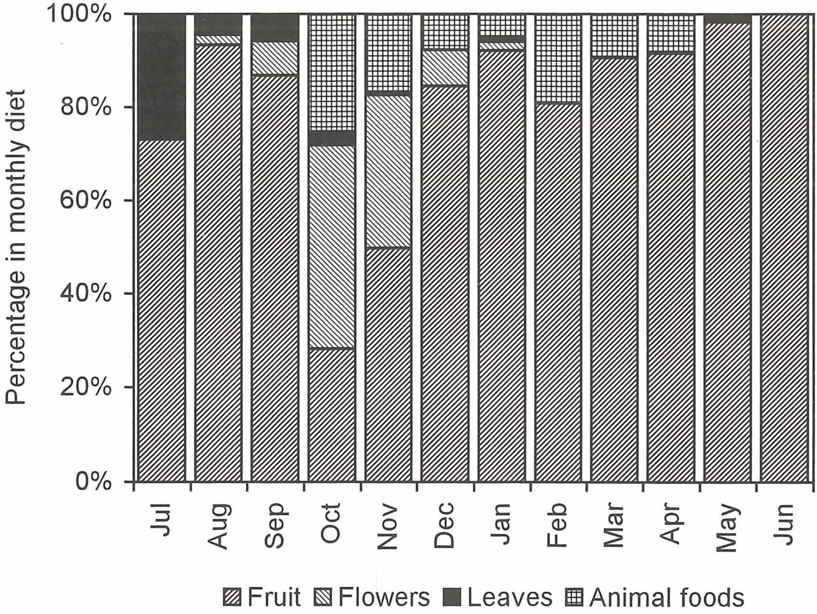

Figure 4.1. Percentage of fruit, flowers, leaves and animal foods in the monthly diet of Regent Bowerbirds ($n = 1193$ feeding records; see Table 4.1 for monthly numbers of feeding records).
Abb. 4.1. Prozentualer Anteil von Früchten, Blüten, Blättern und tierischer Nahrung im monatlichen Nahrungsspektrum von Gelbnacken-Laubenvögeln ($n = 1193$ beobachtete Nahrungsaufnahmen; siehe Tab. 4.1 für die Anzahl beobachteter Nahrungsaufnahmen pro Monat).

Foraging on plant material

Three categories of plant material were distinguished: fruit, flowers and leaves.
Feeding on fruit: Fruit constituted 80.7 % of the annual diet (Table 4.1). Regent Bowerbirds were recorded to take fruits of 62 plant species. Fruits of 18 plant species each constituted more than one per cent of the annual diet. These more important food plants are diverse in both taxonomy and morphology (see Table 4.2). The most important fruits are yellow-red or blue-black. These are the most preferred fruit colours of plant species which rely on seed dispersal by birds (SNOW 1971; VAN DER PIJL 1982; BEEHLER 1983a; SNOW & SNOW 1988).
Regent Bowerbirds did not have a year-round principal food plant species in their diet: Native Olive *Olea paniculata* was an important food source in spring; the figs of *Ficus superba* and *F. platypoda* were important in spring and summer; Native Tamarind *Diploglottis cunninghamii* and Red Ash *Alphitonia excelsa* were important in summer; Blueberry Ash *Elaeocarpus obovatus*, Celery Wood *Polyscias elegans* and Sweet Pittosporum *Pittosporum undulatum* were important in autumn; and the Giant Stinging

Tree *Dendrocnide excelsa* was important in winter. However, most of these species did not fruit annually: for example, *Diploglottis cunninghamii* bore good crops in summer 1989 and 1991, but did not fruit in 1990; *Olea paniculata* produced a good crop in spring 1990, but bore only small crops in 1989 and 1991; *Dendrocnide excelsa*, the most important winter fruit, fruited in winter 1990 and 1992 but not in 1989 and 1991.

Table 4.2. Taxonomy and morphology of food plants important in frugivorous foraging of Regent Bowerbirds, i.e. species constituting more than one per cent of the annual diet (% a.d.). Plant species are arranged in taxonomic order.
Tab. 4.2. Taxonomie und Morphologie von für die frugivore Ernährung von Gelbnacken-Laubenvögeln bedeutenden Pflanzen, d.h. der Arten, die im Jahr mehr als ein Prozent des Nahrungsspektrums ('% a.d.') ausmachen. Die Pflanzenarten erscheinen in der Reihenfolge der Systematik des Pflanzenreichs.

Plant species	Botanical family	Life form	Colour, morphology and dimensions of fruit or edible part	% a.d.
Ficus superba	Moraceae	Tree	Reddish figs, 20 mm diameter	8.3 %
Ficus platypoda	Moraceae	Tree	Yellowish figs, 10-20 mm diameter	2.9 %
Ficus macrophylla	Moraceae	Tree	Purplish figs, 20 mm diameter	1.3 %
Dendrocnide excelsa	Urticaceae	Tree	Mass of small, pink achenes	9.6 %
Piper novae-hollandiae	Piperaceae	Liana	Mass of red, ovoid drupes, 5-6 mm long	1.4 %
Pittosporum undulatum	Pittosporaceae	Tree/ shrub	Mass of red seeds enveloped in sticky fluid out of open capsules, 3-4 mm	3.1 %
Jagera pseudorhus	Sapindaceae	Tree	Black seeds with small, basal, cupular aril out of open capsules	1.4 %
Diploglottis cunninghamii	Sapindaceae	Tree	Seeds enclosed in bright orange aril out of open capsules, 8-10 mm diameter	3.3 %
Alphitonia excelsa	Rhamnaceae	Tree	Black drupes, 8-12 mm diameter	3.4 %
Elaeocarpus obovatus	Elaeocarpaceae	Tree	Blue, ovoid drupes, 8-10 mm long	9.6 %
Rhodamnia argentea	Myrtaceae	Tree	Black berries, 6-10 mm diameter	1.6 %
Polyscias elegans	Araliaceae	Tree	Purple drupes, 5-6 mm diameter	5.0 %
Symplocos thwaitesii	Symplocaceae	Tree	Greenish, ovoid drupes, 6-11 mm long	1.3 %
Diospyros pentamera	Ebenaceae	Tree	Yellowish berries, 8-10 mm diameter	1.4 %
Olea paniculata	Oleaceae	Tree	Bluish-black, ovoid drupes, 10 mm long	8.3 %
Premna lignum-vitae	Verbenaceae	Tree	Red drupes, 10-18 mm diameter	1.5 %
Solanum aviculare	Solanaceae	Shrub	Orange-red, obovoid to ellipsoid berries, 20 mm long	1.5 %
Solanum mauritianum	Solanaceae	Shrub	Yellowish berries, 10-15 mm diameter	1.2 %

Regent Bowerbirds generally harvested fruit while perched in a fruiting plant. An observation of an adult male plucking off a ripe black berry of *Jasminum dallachii* while fluttering in front of a fruit cluster of this vine was the only sighting of a bird taking fruit in flight. Most fruits were swallowed completely, and, while the fleshy part was digested, the seed or seeds were left in viable condition while passed through the gut. Only when foraging on large fruits (e.g. large figs of *F. macrophylla*, *F. superba* and *F. watkinsiana*), were Regent Bowerbirds seen to tear off parts from fruits.

Feeding on flowers: Flowers constituted 8.0 % of the annual diet (Table 4.1). The category 'flower' comprises observations of feeding on buds, petals and/or nectar. Regent Bowerbirds were observed feeding on flowers of nine plant species, but it was often difficult to identify which part of a flower birds were feeding on.

Pollen of Silky Oak *Grevillea robusta* accounted for 87.2 % of the flower-feeding records. Trees of this species flowered annually. During the flowering season of *Grevillea robusta*, Regent Bowerbirds were often seen with orange pollen on their foreheads, picked up while feeding on the nectar. Females were seen defending flowering *Grevillea robusta* and *Callistemon viminalis* plants from conspecifics, but both only on one occasion each.

Feeding on leaves: Leaves constituted 3.6 % of the annual diet (Table 4.1). Regent Bowerbirds fed on leaves of four plant species, by tearing bits off and apparently masticating them. Leaves of White Passion Flower *Passiflora subpeltata* and *Pittosporum undulatum* accounted for 91.3 % of the leaf-eating records.

Foraging on animal foods

Animal foods constituted 7.6 % of the annual diet (Table 4.1). The size of prey items ranged from small Hymenoptera, of less than 5 mm body length, up to katydid grasshoppers and Bladder Cicadas *Cystosoma saundersii*, with lengths of up to over 50 mm. However, in only a few of the records of feeding on animal foods could the captured invertebrates be identified. Therefore, animal foods were not subdivided in Table 4.1.

Regent Bowerbirds used a range of methods when foraging on animals (definitions from FORD 1989): gleaning (bird picks prey off a substrate) was the most common method (104 of 144 records), followed by hawking (bird and prey in the air; 34 records), pouncing (bird flies down to prey on the ground; 4 records), snatching (bird in flight, prey on substrate; 1 record) and probing (bill at least partly inserted into substrate; 1 record).

4.3.2 Dietary relationships of Green Catbird, Regent Bowerbird and Satin Bowerbird

Green Catbird, Regent Bowerbird and Satin Bowerbird all have varied diets, with fruit being the chief component. When using DONAGHEY's (1981) method of calculating proportions of food categories directly from the total number of feeding records, fruit constituted 71.6 % of the annual diet of Regent Bowerbirds (854 of 1193 records, see Table 4.1). This figure is similar to DONAGHEY's (l.c.) data on the diets of Green Catbirds and Satin Bowerbirds in the Tooloom Scrub: fruit formed 77.5 % of the diet of Green Catbirds (424 of 547 records) and 66.9 % of the diet of Satin Bowerbirds (192 of 287 records). According to these data, the proportion of fruit in the annual diet did not differ significantly between the three species (χ^2 = 1.893, *d.f.* = 2, P = 0.388).

Records of fruit-eating of the three species in the Sarabah Range are summarized in Table 4.3. A total of 1881 records of frugivorous foraging was gathered: 270 records of Green Catbirds, 854 records of Regent Bowerbirds and 757 records of Satin Bowerbirds. As these data come from sympatric populations of the three species, a direct comparison of their patterns of frugivory is possible.

Table 4.3. Fruit-eating of sympatric Green Catbirds, Regent Bowerbirds and Satin Bowerbirds. Number and proportion (in brackets) of feeding records of each fruit species. Abbreviations for fruit classes are: C = capsule, D = drupe/berry, F = fig. * = introduced species.
Tab. 4.3. Fruchtnahrung sympatrischer Grünkatzenvögel, Gelbnacken-Laubenvögel und Seidenlaubenvögel. Anzahl und Anteil (in Klammern) jeder Fruchtart an den beobachteten Frucht-Nahrungsaufnahmen. Abkürzungen der Fruchtgruppen: C = Streufrucht, D = Saftfrucht, F = Feige. * = eingeführte Art.

Fruit species	Class	Green Catbird	Regent Bowerbird	Satin Bowerbird
Acacia maidenii	C	0	1 (0.001)	0
Acmena brachyandra	D	2 (0.007)	1 (0.001)	2 (0.003)
Acmena smithii	D	0	2 (0.002)	2 (0.003)
Acronychia oblongifolia	D	6 (0.022)	10 (0.012)	4 (0.005)
Akania lucens	C	0	4 (0.005)	4 (0.005)
Alangium villosum	D	3 (0.011)	6 (0.007)	0
Alphitonia excelsa	D	1 (0.004)	45 (0.053)	26 (0.034)
Amylotheca dictyophleba	D	0	2 (0.002)	0
Archontophoenix cunninghamiana	D	2 (0.007)	0	0
Brachychiton acerifolius	C	1 (0.004)	6 (0.007)	2 (0.003)
Carissa ovata	D	0	1 (0.001)	1 (0.001)
Cayratia clematidea	D	0	2 (0.002)	0
Cayratia eurynema	D	0	3 (0.004)	3 (0.004)
Cephalaralia cephalobotrys	D	0	1 (0.001)	0
Cissus antarctica	D	3 (0.011)	5 (0.006)	15 (0.020)
*Citrus limon**	D	1 (0.004)	1 (0.001)	0
Cordyline petiolaris	D	0	2 (0.002)	0
Cordyline rubra	D	0	1 (0.001)	0
Cryptocarya bidwillii	D	0	2 (0.002)	2 (0.003)
Cudrania cochinchinensis	D	0	10 (0.012)	0
Dendrocnide excelsa	D	30 (0.111)	47 (0.055)	52 (0.069)
Dianella caerulea	D	0	5 (0.006)	2 (0.003)
Diospyros ferrea	D	0	4 (0.005)	0
Diospyros pentamera	D	13 (0.048)	18 (0.021)	32 (0.042)
Diplocyclos palmatus	D	0	5 (0.006)	0
Diploglottis cunninghamii	C	18 (0.067)	42 (0.049)	44 (0.058)

Table 4.3 (continued). – Tab. 4.3 (Fortsetzung).

Fruit species	Class	Green Catbird	Regent Bowerbird	Satin Bowerbird
*Duchesnea indica**	D	0	4 (0.005)	6 (0.008)
Dysoxylum rufum	C	0	4 (0.005)	0
Ehretia acuminata	D	2 (0.007)	3 (0.004)	2 (0.003)
Elaeocarpus obovatus	D	43 (0.159)	113 (0.132)	113 (0.149)
Elattostachys xylocarpa	C	0	4 (0.005)	14 (0.018)
Ficus coronata	F	0	2 (0.002)	1 (0.001)
Ficus fraseri	F	0	2 (0.002)	0
Ficus macrophylla	F	5 (0.019)	18 (0.021)	15 (0.020)
Ficus obliqua	F	0	7 (0.008)	0
Ficus platypoda	F	2 (0.007)	44 (0.052)	32 (0.042)
Ficus superba	F	19 (0.070)	79 (0.093)	44 (0.058)
Ficus watkinsiana	F	29 (0.107)	12 (0.014)	35 (0.046)
Jagera pseudorhus	C	0	15 (0.018)	1 (0.001)
Jasminum dallachii	D	0	1 (0.001)	0
*Lantana camara**	D	0	1 (0.001)	1 (0.001)
Litsea reticulata	D	0	1 (0.001)	1 (0.001)
Melia azedarach	D	2 (0.007)	3 (0.004)	0
Mischocarpus anodontus	C	0	5 (0.006)	0
Morinda jasminoides	D	0	2 (0.002)	0
Olea paniculata	D	18 (0.067)	100 (0.117)	102 (0.135)
Phaleria chermsideana	D	1 (0.004)	0	0
*Physalis peruviana**	D	0	0	2 (0.003)
*Phytolacca octandra**	D	0	3 (0.004)	1 (0.001)
Piper novae-hollandiae	D	19 (0.070)	19 (0.022)	24 (0.032)
Pittosporum undulatum	C	0	27 (0.032)	0
Polyscias elegans	D	22 (0.081)	43 (0.050)	41 (0.054)
Premna lignum-vitae	D	5 (0.019)	8 (0.009)	2 (0.003)
Pseudocarapa nitidula	C	4 (0.015)	0	12 (0.016)
Rapanea howittiana	D	0	0	1 (0.001)
Rhodamnia argentea	D	3 (0.011)	22 (0.026)	22 (0.029)
Rhodomyrtus psidioides	D	0	0	1 (0.001)
Rubus moluccanus	D	0	5 (0.006)	0
Rubus rosifolius	D	0	4 (0.005)	1 (0.001)
Sarcopteryx stipata	C	2 (0.007)	5 (0.006)	0
Scolopia braunii	D	3 (0.011)	9 (0.011)	12 (0.016)
Solanum aviculare	D	6 (0.022)	13 (0.015)	39 (0.052)
*Solanum mauritianum**	D	0	17 (0.020)	1 (0.001)
*Solanum nigrum**	D	0	3 (0.004)	0
Symplocos thwaitesii	D	5 (0.019)	18 (0.021)	13 (0.017)
Synoum glandulosum	C	0	4 (0.005)	0
Tetrastigma nitens	D	0	7 (0.008)	27 (0.036)
Trochocarpa laurina	D	0	1 (0.001)	0
Total		270 (1.000)	854 (1.000)	757 (1.000)

The three species combined were recorded to take fruits of 68 plant species, 49 (72.1 %) of which were categorized as drupe/berry, 12 (17.6 %) as capsule and 7 (10.3 %) as fig. Green Catbirds took fruits of 29 species, Satin Bowerbirds of 42 species and Regent Bowerbirds of 62 species. The niche breadths of frugivorous foraging were 0.18 for Green Catbirds, 0.21 for Satin Bowerbirds and 0.25 for Regent Bowerbirds. Thus, Green Catbirds were slightly more specialized in their fruit-eating than the other two species. The three species showed considerable niche overlap in their frugivorous foraging: niche overlap of Green Catbird and Regent Bowerbird was 0.81, overlap of Green Catbird and Satin Bowerbird was 0.88, and overlap of Regent Bowerbird and Satin Bowerbird was 0.93. Thus, the bower-building Regent and Satin Bowerbirds showed more dietary overlap between themselves than either did with the monogamous Green Catbird.

The proportional frequencies of fruit from the three morphological classes fig, drupe/berry and capsule in the fruit-eating of the three species are summarized in Table 4.4. The proportions of fruit from the three classes differed significantly, though only slightly, between the three species (3x3 contingency analysis, $\chi^2 = 9.825$, *d.f.* = 4, $P < 0.05$). When testing differences in the proportion of a fruit class between pairs of species in 2x2 contingency analyses, the only significant differences were a higher proportion of the drupe/berry class in the diet of Satin Bowerbirds compared to Regent Bowerbirds ($\chi^2 = 6.764$, *d.f.* = 1, $P < 0.01$) and a higher proportion of capsular fruits in the diet of Regent Bowerbirds compared to Satin Bowerbirds ($\chi^2 = 4.717$, *d.f.* = 1, $P < 0.03$). None of the differences in the consumption of fruit from the three morphological classes between Green Catbirds and either of the two bower-building species was significant. In all three species, by far the most fruits consumed were of the morphological class drupe/berry. However, this does not take biomass eaten into account.

Table 4.4. Consumption of fruit from three morphological classes by sympatric Green Catbirds, Regent Bowerbirds and Satin Bowerbirds. Total number and percentage (in brackets) of feeding records.

Tab. 4.4. Verzehr von Früchten dreier morphologischer Gruppen durch sympatrische Grünkatzenvögel, Gelbnacken-Laubenvögel und Seidenlaubenvögel. Anzahl und prozentualer Anteil (in Klammern) beobachteter Nahrungsaufnahmen.

Morphological fruit class	Green Catbird	Regent Bowerbird	Satin Bowerbird
Fig	55 (20.4 %)	164 (19.2 %)	127 (16.8 %)
Drupe/berry	190 (70.4 %)	573 (67.1 %)	553 (73.0 %)
Capsule	25 (9.2 %)	117 (13.7 %)	77 (10.2 %)
Total	270 (100 %)	854 (100 %)	757 (100 %)

4.4 Discussion

Foods of the Regent Bowerbird

Regent Bowerbirds were observed to forage on a great variety of plant material and animal foods (Table 4.1). The diet was found to be primarily frugivorous with fruit of many different plant species comprising the bulk of the diet in most months, whereas flowers, leaves and animals figured prominently in only few months (Fig. 4.1).

Large numbers of plant species are not unusual in diets of frugivores: for example, SNOW (1962a) found 105 fruit species in the diet of White-bearded Manakins *Manacus manacus*, INNIS & MCEVOY (1992) found fruits of 104 species in the diet of Green Catbirds. Table 4.1 contains a large number of fruit species Regent Bowerbirds were only rarely observed to feed on; this may indicate that the list of fruit species taken by this species is not yet complete. FLOYD (1990) and HOLMES (1990) name a few additional species of fruit Regent Bowerbirds have been observed to feed on in other areas.

Despite the predominance of fruit in the annual diet of Regent Bowerbirds, the largest number of feeding records for a particular food item was obtained for nectar of *Grevillea robusta*. DONAGHEY (1981) observed flower-eating by Green Catbirds and Satin Bowerbirds but did not see them feeding on nectar. The thinner bills of Regent Bowerbirds may be more suitable for nectar-feeding than the stouter bills of the other two species. However, VELLENGA & VELLENGA (1985) regularly observed Satin Bowerbirds feeding on nectar of *Banksia* spp. in heathland. Observations of Regent Bowerbirds defending flowers suggest that they may be a particularly valuable food resource. Reports of frugivores defending fruit-bearing plants are much rarer than reports of birds defending flowers (PRATT 1984).

The importance of leaves in the diet of catbirds and bowerbirds has long been overlooked. Several species are now known to feed on leaves regularly, particularly in the winter months (LAVERY & GRIMES 1974; MARCHANT 1974; FRITH & FRITH 1979; DONAGHEY 1981; VELLENGA & VELLENGA 1985; BARKER & VESTJENS 1990). DONAGHEY (1981) found that Satin Bowerbirds were significantly more folivorous and less frugivorous in woodland than in rainforest. Most leaf-eating by Satin Bowerbirds was observed between July and October, the months with the lowest numbers of plant species in fruit (DONAGHEY l.c.). In this study, most observations of leaf-eating Regent Bowerbirds were also made between July and October. It appears that leaves are mainly taken when more valuable food items are in short supply.

Dietary relationships of catbirds and bowerbirds

Several authors have emphasized that the term 'frugivore' conceals two important distinctions that need to be made: (a) the distinction between generalized frugivores and specialized frugivores; and (b) the distinction between seed dispersers and seed predators, the latter taking fruit in order to digest the seeds, often discarding the fleshy parts (SNOW 1971, 1980; HOWE & ESTABROOK 1977; DIAMOND 1986b; BEEHLER 1991).

The three studied species of the bowerbird family were all found to be mainly frugivorous, with fruit comprising similar proportions of their annual diets. The closely-related, bower-building Regent and Satin Bowerbirds showed more overlap in their frugivorous diets among themselves than with the monogamous Green Catbird. However, dietary overlap between all three species was considerable and was the most prominent feature of their diets. Thus, the three species are generalized frugivores.

Catbirds and bowerbirds generally consume fleshy fruits and leave the seeds in viable condition (FLOYD 1990; INNIS & MCEVOY 1992; this study). They have short foraging bouts and take only few fruits per bout (DONAGHEY 1981; INNIS & MCEVOY 1992; GREEN 1993). This behaviour and the frequent alternation of food plants assist in the dispersal of seeds (BEEHLER 1983a, 1991). In view of the great variety of species of fruit consumed by catbirds and bowerbirds (Table 4.3; DONAGHEY 1981; INNIS & MCEVOY 1992), they are important seed dispersers. Regent Bowerbirds, for example, have been suspected as potential seed dispersers of *Acronychia oblongifolia*, *Diospyros pentamera*, *Diploglottis cunninghamii*, *Elaeocarpus obovatus* and *Polyscias elegans* (FLOYD 1990; R.J. GREEN pers. comm.). Catbirds and bowerbirds may occasionally damage seeds when foraging on unripe fruit. For example, Regent and Satin Bowerbirds consumed both unripe green and ripe bluish-black fruits of *Olea paniculata* in spring 1990. However, *Olea paniculata* had produced a large crop in that year, and the number of seeds left in viable condition probably far outnumbered the damaged ones.

The considerable niche overlap in the fruit-eating by Green Catbirds, Regent Bowerbirds and Satin Bowerbirds does not necessarily imply intense competition between the three species. Instead, there may be an inverse relationship between niche overlap and competition: if resources are not in short supply, extensive niche overlap may be correlated with reduced competition (PIANKA 1974). Moreover, each species may take fruits of different size or from different locations.

The monogamous Green Catbirds were found to have a slightly narrower diet niche breadth than the two non-monogamous bowerbird species. However, the differences in diet niche breadth between the three species may simply reflect the differences in the number of feeding records for each species. In a long-term study drawing on data from more than ten years, INNIS & MCEVOY (1992) have shown that the number of fruit species taken by Green Catbirds is not smaller than in non-monogamous bowerbird species.

Fruits of the morphological class drupe/berry predominated in the frugivorous foraging of all three species studied in the Sarabah Range (Tables 4.3-4.4). This comparison does not take biomass eaten into account, but a predominance of drupes and berries corresponds with available information on the foods of other species of the bowerbird family (PRUETT-JONES & PRUETT-JONES 1985; BEEHLER 1988, 1991; FRITH & FRITH 1990c; BARKER & VESTJENS 1990; R.J. GREEN pers. comm.).

Most species in the bowerbird family are similar in bill shape and skull morphology (STONOR 1937; BOCK 1963), the bill of the Tooth-billed Bowerbird being a notable exception (MARSHALL 1951a; LAVERY & GRIMES 1974). Birds of paradise show much more variation in morphology (BOCK 1963; DIAMOND 1986b; BEEHLER 1988; FRITH & BEEHLER 1998). The large number of frugivores in New Guinea may have caused great selective pressure for specialization: for example, the complete guild of frugivores in the Sarabah Range consists of 11 species (Appendix 2), whereas 10 bird of paradise species alone (plus many other frugivores) occur in BEEHLER's (1983a) study area in New Guinea. However, most morphological specializations in birds of paradise appear to be related to the insectivorous part of their diets (COOPER & FORSHAW 1977; DIAMOND 1986b; BEEHLER 1988). Only few species are specialized frugivores, and these are species with a monogamous mating system: Crinkle-collared Manucode *Manucodia chalybata* and Trumpet Manucode *M. keraudrenii* are fig specialists (BEEHLER 1983a, 1985a), Macgregor's Bird of Paradise *Macgregoria pulchra* is specialized on fruit of the podocarp *Dacrycarpus compactus* (BEEHLER 1983b).

DONAGHEY (1981) suggested that the monogamous Green Catbird may also be a fig specialist. In the Sarabah Range, the percentage of figs was slightly higher in the diet of Green Catbirds than in Regent and Satin Bowerbirds (Table 4.4), but this difference was not significant. The only significant differences in the dietary proportion of a fruit class between pairs of species were found between the two bower-building species. As figs accounted for only 20.4 % of the frugivorous foraging of Green Catbirds in this study (Table 4.4), it is doubtful that fig trees could be a sufficient, economically-defendable food resource for territorial Catbirds in the Sarabah Range.

Figs were more important in two populations of Green Catbirds studied by INNIS & MCEVOY (1992), where figs accounted for 33.8 % and 39.6 % of the feeding records respectively. While these percentages are almost twice as large as the 20.4 % found in this study, they are much lower yet than the percentages found in manucodes: figs accounted for 93 % of the frugivorous foraging of Crinkle-collared Manucodes and for 80 % in Trumpet Manucodes (BEEHLER 1983a). Compared to these large percentages, it appears inappropriate to describe the Green Catbird as a fig 'specialist'.

Many of the plant species important in frugivorous foraging of catbirds and bowerbirds in the Sarabah Range do not produce good crops in annual cycles: *Diploglottis cunninghamii*, for example, appears to be a species with biennial fruiting, as trees fruited in 1987, 1989 and 1991, but not in 1986, 1988 and 1990; *Dendrocnide excelsa* fruited almost strictly every two years, in 1985, 1987, 1988, 1990 and 1992, but not in 1986, 1989 and 1991; *Olea paniculata* fruited irregularly, between 1985 and 1991 there was only one large crop, in 1990, and several smaller crops; *Ficus superba* produced several good crops, but at irregular intervals (R.J. CHURCH pers. comm.). The considerable year-to-year differences in fruit crops of particular species make firm statements about food preferences extremely difficult. The diets of the three species studied showed much more similarities than differences. However, the differences may be more pronounced between the nestling diets of monogamous and non-monogamous species of the bowerbird family (see Chapter 8).

Some fruit was available in every month in the Sarabah Range. But a good crop of one species does not necessarily substitute for a poor crop of another species, as fruits of different species can differ considerably in their nutritional value (CROME 1975). For example, capsular arillate fruits, such as *Diploglottis cunninghamii*, may be richer in proteins and lipids than simpler and smaller fruits; the nutritional value of some fruits (of a particular species or of particular plants of one species) may be augmented because their pericarp is infested with insect larvae (CROME l.c.).

Unpredictability in the availability of fruit of a particular species or quality may have been a factor precluding bowerbirds from economically defending territories and, thus, promoting non-monogamous mating systems. However, frugivory does not constitute the sole sufficient factor promoting male emancipation; there is no simple dichotomy between diets of monogamous and non-monogamous species (BRADBURY 1981; BEEHLER 1983a; FRITH & BEEHLER 1998). The relationship between frugivory and polygamy is complex (BEEHLER 1987, 1988, 1991), and only very rarely can simple rules explain why closely-related bird species differ in their mating systems.

5 Population Parameters and their Implications for the Reproductive Biology

5.1 Introduction

Size and composition of a population are influenced by the demographic processes, birth, death and migration (BEGON et al. 1986). Population parameters, such as sex ratio, age structure, survivorship and longevity, are likely to affect the opportunity for mate choice and sexual selection (PARTRIDGE & ENDLER 1987). Therefore, knowledge of demographic patterns is important in understanding the determinants of mating systems and mating strategies.

The absolute sex ratio, the ratio of males to females in the overall population, does not include considerations of whether individuals are sexually active or not. This is taken into account when estimating the operational sex ratio, the ratio of fertilizable females to sexually active males (EMLEN & ORING 1977). To estimate the operational sex ratio of a population, knowledge of both the absolute sex ratio and the age structure of the population is required. The operational sex ratio provides an empirical measure of the potential for individuals to monopolize mates; for instance, multiple mating opportunities for individual males may be expected where the operational sex ratio is female-biased (EMLEN & ORING l.c.).

Considering the potential of population parameters in estimating the extent and nature of evolution by sexual selection, there are surprisingly few cases where demographic differences between the sexes have been thoroughly investigated (SUTHERLAND 1987; PARTRIDGE & ENDLER 1987). One of the demographic processes where sex differences have been studied is dispersal. In most bird species females disperse more than males, whereas males are usually the main dispersers among mammals. This sex difference in dispersal of birds and mammals has been linked to the differences in their mating systems: most bird species are monogamous, whereas most species of mammals are polygamous (GREENWOOD 1980; BEGON et al. 1986; see Chapter 1).

Population parameters have been largely neglected in studies and reviews on the reproductive biology and evolutionary ecology of bowerbirds (e.g. BORGIA 1985a,b, 1986a, 1995a,b; BORGIA et al. 1985; DIAMOND 1986b; BACKUS 1987; MÜLLER 1990; JOHNSGARD 1994; PRUETT-JONES & PRUETT-JONES 1994). DONAGHEY (1981), in his study on the mating systems of Green Catbirds and Satin Bowerbirds, found evidence of high annual survival rates in both species, but did not study any other population parameters. In this chapter the population parameters sex ratio, age structure, survivorship, longevity and movements are investigated, in order to provide empirical measures of the potential for polygamy in the Regent Bowerbird.

5.2 Materials and methods

Several thousand sightings and more than one hundred re-traps of Regent Bowerbirds from the colour-banded population in the Sarabah Range made the calculation of several population parameters possible. Following WOINARSKI & TIDEMANN (1992), data of sightings and re-traps of each individual were tabulated to derive the percentages of individuals known to be alive in successive months following banding, in order to plot survivorship curves.

Mean annual survival rates, S, were estimated using a measure adopted from BOEHM (1974), NICHOLLS & WOINARSKI (1988) and NOSKE (1991), based on LACK (1954):

$$S = 100 \frac{\sum_{i=1}^{n} b_{i+1}}{\sum_{i=1}^{n-1} a_i}$$

where a is the number of banded birds present in study year i, and b is the number of birds still present one year later, in year $i+1$.

Survival was also calculated as mean monthly survival rates, s, using the measure of NICHOLLS & WOINARSKI (1988) and WOINARSKI & TIDEMANN (1992):

$$s = 100 \frac{\sum_{i=2}^{n} KTBA_i}{\sum_{i=1}^{n-1} KTBA_i}$$

where $KTBA$ is the percentage of individuals "*known to be alive*" in n successive months following banding. However, this measure produced some rather meaningless mean monthly survival rates of over 100 % (due to the fact that $KTBA$ percentages of birds banded early in this study were higher than those of birds banded later), which could not be used for further analyses.

Mean annual mortality rates, M, can be calculated from mean annual survival rates, S, as $M = 100 - S$ (NICHOLLS & WOINARSKI 1988). Therefore, mean monthly mortality rates, m, are:

$$m = \frac{100 - S}{12}$$

Expectation of further life, E, is a function of mortality (FRY 1980) and was calculated using the formula of LACK (1954):

$$E = \frac{200 - m}{2m}$$

where m is the mean monthly mortality rate, which is assumed to be constant throughout the year.

Individuals could be grouped in sex and age classes according to the sex-related and age-related variation in morphology and plumage described in Chapter 3. In this chapter and in the following chapters, males in first- and second-year plumage are called immature, males in third-, fourth-, fifth- and sixth-year plumage are called subadult, seventh-year and older males are called adult.

Survivorship of sex and age classes was compared by testing the significance of differences between percentages of individuals known to be alive in successive months following banding with Mann-Whitney *U*-tests. As all sample sizes were above 21, Mann-Whitney *U*-tests for large samples were used (SPATZ & JOHNSTON 1989).

Appeals to report any sightings of colour-banded birds were publicized at the Green Mountains Ranger Station and at O'Reilly's Mountain Resort (both in Lamington National Park, 7.5 km south-south-east of the banding site), at the nearest post office and tourist information bureau (both in Canungra, 17.5 km north-north-east of the banding site) and in the newsletter of the Royal Australasian Ornithologists Union (LENZ 1991).

The period of three years of field work was too short to obtain data on maximum longevity of Regent Bowerbirds. Therefore, additional longevity records of individuals banded and re-trapped in New South Wales were obtained from the ABBBS on microfiches (see Appendix 5). Most of the 127 re-traps were made in the Iluka Nature Reserve, at Tumbi Umbi and near Kincumber in New South Wales (for descriptions of these areas see LANE 1969; ADAM 1987).

For an assessment of the reproductive status of males of different age classes, testis measurements were obtained from zoological museum collections. Labels of museum specimens gave the size of testes as length by width. In order to allow a direct comparison of the size of testes, their volume, V, was calculated using the geometric formula for the volume of rotating ellipsoids (SIEBER & HUBER 1974):

$$V = \frac{4}{3}\pi \cdot ab^2$$

where a is half of the length and b is half of the width.

5.3 Results

Sex ratio and age structure of the overall population

The Regent Bowerbird population in the Sarabah Range had a balanced absolute sex ratio: 101 of the 203 individuals banded (49.8 %) were males, 102 individuals (50.2 %) were female (see Appendix 3).

Data on sex ratio and age structure are presented in Table 5.1. In all three mating and breeding seasons studied, males slightly outnumbered females, but this did not differ significantly from a balanced absolute sex ratio (3x2 contingency analysis, $\chi^2 = 0.054$, *d.f.* = 2, $P = 0.97$). In the third season studied, there were significantly fewer immature males ($\chi^2 = 3.982$, *d.f.* = 1, $P < 0.05$) and significantly fewer first-year females ($\chi^2 = 4.060$, *d.f.* = 1, $P < 0.05$) in the population than in the previous season. None of the other, slight, differences in the percentages of age classes between years were significant (2x2 contingency analyses, *d.f.* = 1, all $P >> 0.05$).

Thus, although the total number of observed birds varied between years, the sex ratio and age structure of the population was very similar in each of the three years studied. The three-year means of the percentages of males, females and all age classes are also given in Table 5.1.

Table 5.1. Sex ratio and age structure of the Regent Bowerbird population in the Sarabah Range. Number and percentage (in brackets) of individuals of several sex and age classes during the mating and breeding seasons 1989, 1990 and 1991.

Tab. 5.1. Geschlechterverhältnis und Altersaufbau der Gelbnacken-Laubenvogel-Population in der Sarabah-Bergkette. Anzahl und prozentualer Anteil (in Klammern) von Individuen mehrerer Geschlechts- und Altersklassen während der Paarungs- und Brutsaisons 1989, 1990 und 1991.

Class	1989	1990	1991	Mean
All males	38 (52.8 %)	61 (51.3 %)	75 (52.4 %)	52.1 %
All females	34 (47.2 %)	58 (48.7 %)	68 (47.6 %)	47.9 %
Immature males	7 (9.7 %)	16 (13.5 %)	8 (5.6 %)	9.6 %
Subadult males	18 (25.0 %)	27 (22.7 %)	38 (26.5 %)	24.7 %
Adult males	13 (18.1 %)	18 (15.1 %)	29 (20.3 %)	17.8 %
First-year females	13 (18.1 %)	12 (10.1 %)	5 (3.5 %)	10.6 %
Older females	21 (29.1 %)	46 (38.6 %)	63 (44.1 %)	37.3 %

Survivorship and longevity

Survivorship data are presented in Table 5.2 and Figures 5.1 to 5.3. Mean annual survival rates were higher in males than in females; in both males and females, survival rates were higher in older birds than in younger ones (Table 5.2).

Table 5.2. Survivorship of Regent Bowerbirds in the Sarabah Range, based on three years of observation. Mean annual survival rates (*S*), mean monthly mortality rates (*m*) and expectation of further life (*E*) of several sex and age classes.
Tab. 5.2. Überlebensdaten von Gelbnacken-Laubenvögeln in der Sarabah-Bergkette, basierend auf drei Untersuchungsjahren. Mittlere jährliche Überlebensraten (*S*), mittlere monatliche Sterberaten (*m*) und Lebenserwartung (*E*) mehrerer Geschlechts- und Altersklassen.

Class	*S*	*m*	*E*
All males	73.7 %	2.2 %	45.2 months
All females	63.0 %	3.1 %	32.0 months
Immature males	52.2 %	4.0 %	24.6 months
Subadult males	75.6 %	2.0 %	48.5 months
Adult males	87.1 %	1.1 %	92.1 months
First-year females	40.0 %	5.0 %	19.5 months
Older females	71.6 %	2.4 %	41.9 months

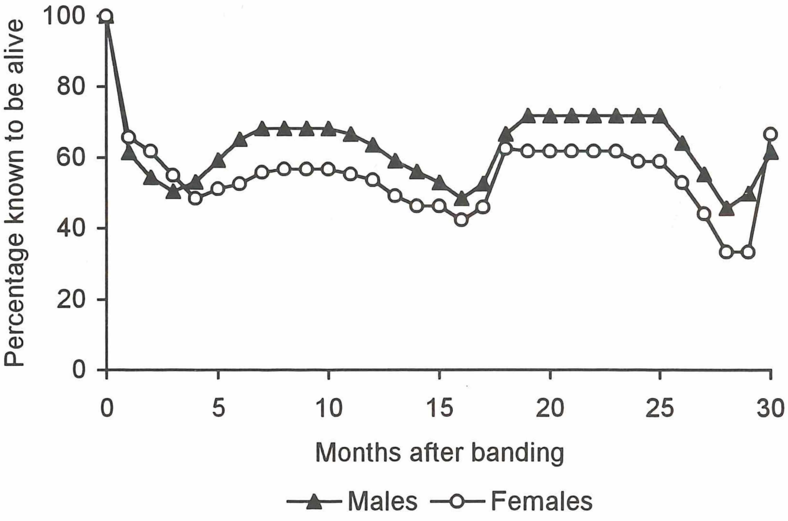

Figure 5.1. Survivorship curves of male and female Regent Bowerbirds in the Sarabah Range (percentages known to be alive in successive months following banding).
Abb. 5.1. Überlebenskurven von männlichen und weiblichen Gelbnacken-Laubenvögeln in der Sarabah-Bergkette (prozentualer Anteil der als noch am Leben bekannten Individuen in den Monaten nach der Beringung).

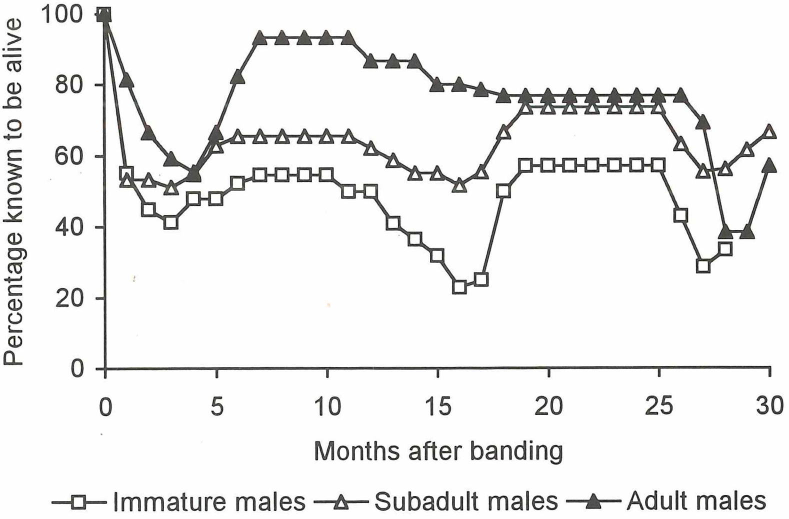

Figure 5.2. Survivorship curves of immature, subadult and adult male Regent Bowerbirds in the Sarabah Range (percentages known to be alive in successive months following banding).
Abb. 5.2. Überlebenskurven von immaturen, subadulten und adulten männlichen Gelbnacken-Laubenvögeln in der Sarabah-Bergkette (prozentualer Anteil der als noch am Leben bekannten Individuen in den Monaten nach der Beringung).

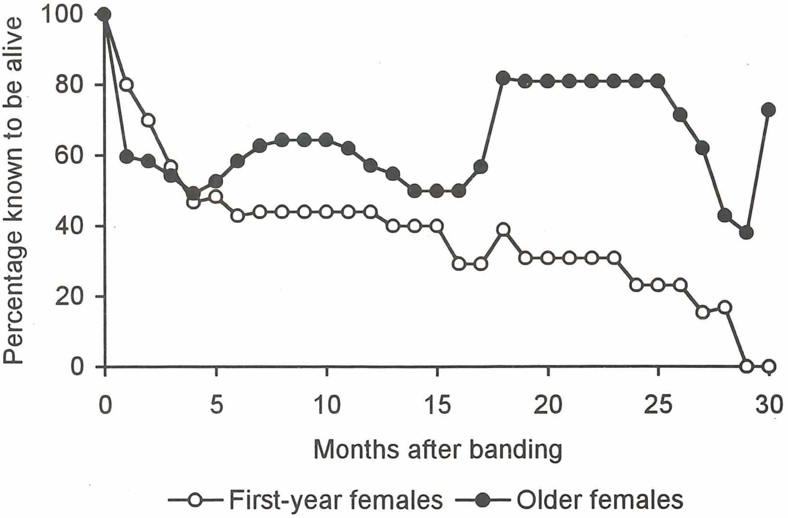

Figure 5.3. Survivorship curves of first-year and older female Regent Bowerbirds in the Sarabah Range (percentages known to be alive in successive months following banding).
Abb. 5.3. Überlebenskurven von weiblichen Gelbnacken-Laubenvögeln im ersten Lebensjahr und von älteren Weibchen in der Sarabah-Bergkette (prozentualer Anteil der als noch am Leben bekannten Individuen in den Monaten nach der Beringung).

All differences in survivorship between sex and age classes were highly significant: the percentage of individuals known to be alive in successive months following banding (see Figs 5.1-5.3) was significantly higher in males than in females (Mann-Whitney *U*-test, $n_1 = 30$, $n_2 = 30$, $z = -3.184$, $P < 0.002$), higher in adult males than in subadult males (Mann-Whitney *U*-test, $n_1 = 30$, $n_2 = 30$, $z = -4.533$, $P < 0.00001$), higher in subadult males than in immature males (Mann-Whitney *U*-test, $n_1 = 30$, $n_2 = 28$, $z = -5.078$, $P < 0.00001$), and higher in second-year and older females than in first-year females (Mann-Whitney *U*-test, $n_1 = 30$, $n_2 = 30$, $z = -5.584$, $P < 0.00001$).

In accordance with the differences in survival and mortality rates, the calculated expectation of further life is higher in males than in females, and, in both males and females, life expectation is higher in older birds than in younger ones (see Table 5.2). Males which survived the relatively high juvenile mortality have an expectation of 92.1 months of further life as adults, i.e. almost eight years.

The activities of bird banders in New South Wales have not been persistent enough to construct accurate life tables for Regent Bowerbirds. Longevity records of some individuals banded and re-trapped in New South Wales are presented in Table 5.3. These longevity records confirm that Regent Bowerbirds are very long-lived passerines and that survivorship is particularly high in males. The maximum recorded longevity is that of a male Regent Bowerbird (band number 060-51091) re-trapped more than 17 years after banding. On the banding date, the bird bander, P.D. STRONG, described this individual as an adult male (ABBBS microfiche); considering the moult sequences and plumage changes of male Regent Bowerbirds described in Chapter 3, this individual may have been in its 24th year of life, or even older, on the last re-trap date.

Operational sex ratio

An estimate of the operational sex ratio requires knowledge of the percentages of fertilizable females and sexually active males in the population. The mean percentage of adult males in the Regent Bowerbird population in the Sarabah Range was 17.8 % (Table 5.1). This low percentage, only one third of all males, suggests a female-biased operational sex ratio.

The exact age at which the females start breeding is not known. According to skull examinations by DISNEY & LANE (1971), female Regent Bowerbirds may breed with an incompletely ossified skull. This suggests that female Regent Bowerbirds reach sexual maturity in their second or third year of life, just as female Satin Bowerbirds do (VELLENGA 1980a; DONAGHEY 1981; DONAGHEY et al. 1985).

The mean percentage of second-year and older females in the Sarabah Range population was 37.3 % (Table 5.1). This figure gives an operational sex ratio of 2.1 (37.3 % divided by 17.8 %), assuming that females reach sexual maturity in their second year of life.

The plumage of third-year and older females does not differ from second-year plumage (see Chapter 3). Therefore, the exact percentage of third-year and older females could not be determined. However, the monthly mortality rates of females which survived their first year of life was only 2.4 % (Table 5.2). Thus, even if assuming that some females only reach sexual maturity in their third year of life, the operational sex ratio would be close to 2 fertilizable females to 1 adult male.

Table 5.3. Longevity records of some Regent Bowerbirds banded and re-trapped in New South Wales (all individuals were re-trapped at the locality where they had been banded).
Tab. 5.3. Langlebigkeitsbelege einiger Gelbnacken-Laubenvögel, die in Neusüdwales beringt und wieder gefangen wurden (alle Individuen wurden an ihrem Beringungsort wieder gefangen).

Band number	Date of banding	Date of last re-trap	Time elapsed	Locality
Males:				
060-14889	18 Nov. 1975	12 May 1982	6.5 years	Iluka
060-14895	18 Nov. 1975	14 Apr. 1984	8.4 years	Iluka
060-19887	24 Sep. 1974	23 Aug. 1979	4.9 years	Iluka
060-22815	01 Sep. 1969	01 Dec. 1977	8.2 years	Iluka
060-36940	30 Nov. 1962	13 Nov. 1969	7.0 years	Tumbi Umbi
060-51091	30 Sep. 1966	24 Dec. 1983	17.2 years	Iluka
060-77034	29 Aug. 1971	23 Sep. 1981	10.1 years	Kincumber
060-85008	06 Oct. 1975	02 Sep. 1983	7.9 years	Kincumber
060-85018	02 Aug. 1976	04 Nov. 1981	5.3 years	Kincumber
060-85037	30 Sep. 1978	02 Sep. 1983	4.9 years	Kincumber
061-17492	30 Nov. 1977	11 Dec. 1986	9.0 years	Iluka
Females:				
060-29211	01 Oct. 1972	22 Apr. 1978	5.6 years	Tumbi Umbi
060-29278	27 Oct. 1974	22 Mar. 1981	6.4 years	Tumbi Umbi
060-76746	27 Dec. 1974	23 Sep. 1981	6.7 years	Kincumber
060-77039	29 Aug. 1971	02 Aug. 1976	4.9 years	Kincumber
061-06489	29 Oct. 1978	31 Dec. 1984	6.2 years	Iluka
061-09264	20 Sep. 1976	12 May 1982	5.6 years	Iluka
061-46511	19 Nov. 1983	23 Nov. 1989	6.0 years	Pappinbarra

This estimate of the operational sex ratio is based on the assumption that only males in full adult plumage are sexually active. To assess the reproductive status of males of different age, the size of their testes was compared. The change in testis size in Regent Bowerbirds from various localities in north-eastern New South Wales is shown in Fig. 5.4. Testis size varied with both age and season. In adult males, testis size varied from approximately 6 mm^3 in winter (May and June) to 600 mm^3 during the peak of the mating season (November and December). Testes of immature males were considerably smaller than those of adult birds and reached only a quarter of the volume of adult testes at the peak of the mating season (note logarithmical scale of the y-axis in Fig. 5.4). Several testis measurements of subadult males, however, were in the order of adult birds. Thus, some subadult males may have fully-developed gonads and may be capable of successful reproduction, although still lacking the bright plumage of adult males.

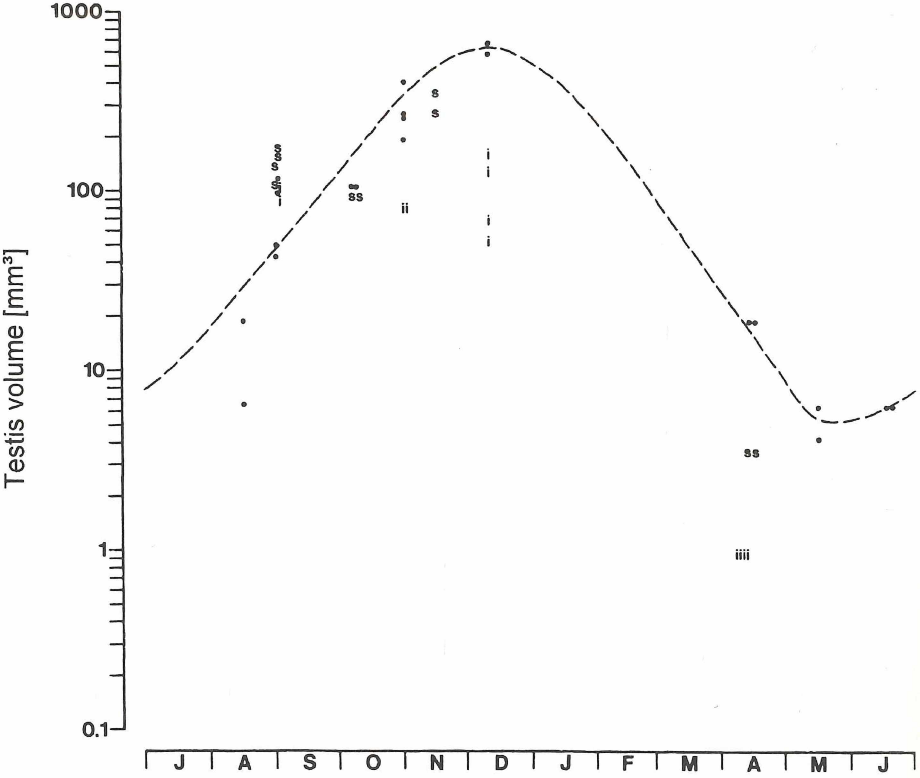

Figure 5.4. Change in testis size in Regent Bowerbirds during the year (data of museum specimens from various localities in north-eastern New South Wales). Testis volumes (in mm³) of immature (= i; n = 12), subadult (= s; n = 10) and adult males (= dots and broken line; n = 20), collected at different times of the year.

Abb. 5.4. Veränderung der Hodengröße bei Gelbnacken-Laubenvögeln im Jahreslauf (Daten von Museumsbälgen verschiedener Lokalitäten im nordöstlichen Neusüdwales). Hodenvolumina (in mm³) von immaturen (= i; n = 12), subadulten (= s; n = 10) und adulten Männchen (= Punkte und gestrichelte Linie; n = 20), die zu unterschiedlichen Zeitpunkten im Jahreslauf gesammelt wurden.

Movements

Of the 203 Regent Bowerbird individuals banded in the Sarabah Range, twelve (= 5.9 %) were observed at locations outside the study area (see Table 5.4): nine individuals were observed at a location 2.5 km to the south of the banding site (as the bowerbird flies), two individuals were observed at a location 7.5 km south-south-east of the banding site, and one individual was observed at both these locations. Three individuals (GRG, GOO and WBO) returned to the study area after they had been observed at the location 2.5 km south of the banding place.

Five of the twelve individuals observed outside the study area were males and seven were females. No age class predominated among them. However, none of the banded adult males was ever observed outside the study area.

Of the 127 Regent Bowerbird re-traps on ABBBS microfiches, 126 were made at the banding location, one immature male was re-trapped 1.8 km away from the banding location. In addition to the data on microfiche, one female was found 7 km from the banding place (ANON. 1981).

Therefore, although more than 800 Regent Bowerbird individuals have been banded during the last three decades (ABBBS microfiches and this study), there is no evidence of predominance of one sex in movements of this species. Overall, observations and re-traps of banded individuals give only little evidence of movements of Regent Bowerbirds.

Table 5.4. Movements of Regent Bowerbirds banded in the Sarabah Range study area. Data of twelve individuals observed at locations outside the study area, near the Romeo Lahey Memorial (2.5 km S of banding site) and near the Green Mountains Ranger Station (7.5 km SSE of banding site).

Tab. 5.4. Wanderungen von Gelbnacken-Laubenvögeln, die im Untersuchungsgebiet in der Sarabah-Bergkette beringt wurden. Daten von zwölf Individuen, die außerhalb des Untersuchungsgebiets beobachtet wurden, beim Romeo Lahey Memorial (2,5 km südlich des Beringungsorts) und bei der Green Mountains Ranger Station (7,5 km südsüdöstlich des Beringungsorts).

Colour band combination	Band number	Sex	Age when first observed at location outside study area
Observed near Romeo Lahey Memorial:			
BNB	062-02145	Male	Second-year
GRG	061-95456	Male	Second-year
GON	062-02138	Female	Second-year or older
GOB	062-02101	Male	Third-year
GOO	062-02103	Female	Third-year or older
ONN	061-95465	Female	Second-year or older
OGB	061-95481	Female	Second-year or older
OWR	062-02110	Female	Third-year or older
WRB	062-02265	Male	Sixth-year
WBO	062-02263	Female	Second-year or older
Observed near Green Mountains Ranger Station:			
GBB	061-95477	Male	Fourth-year
GOB	062-02101	Male	Third-year
OOR	061-95491	Female	Third-year or older

5.4 Discussion

Survivorship, longevity and movements

Studies on the population ecology of Australian passerines have frequently revealed high annual survival rates (FORD 1989; ROWLEY & RUSSELL 1991). Data on the survivorship of species of the bowerbird family show particularly high survival rates (Table 5.2), even by Australian standards. Longevity records and survivorship data similar to those of Regent Bowerbirds have also been recorded of Green Catbirds (ANON. 1969b, 1983; DONAGHEY 1981), Tooth-billed Bowerbirds (ANON. 1991; FRITH & FRITH 1995), Golden Bowerbirds (FRITH 1989; ANON. 1991; FRITH & FRITH 1998a) and Satin Bowerbirds (ANON. 1979a, 1992; VELLENGA 1980b; DONAGHEY 1981; BORGIA 1993).

High survival rates are associated with high stability in breeding populations (FORD 1989). This is documented by the similarities of age class percentages in the population of Regent Bowerbirds in the Sarabah Range over the three years investigated (Table 5.1). The only significant differences of age class percentages between years were the smaller numbers of immature males and first-year females in the third year. The low percentages of these, the youngest age classes of males and females, are very likely to have been caused by the unusual drought conditions during the previous year (see Chapter 2), resulting in a low level of recruitment. The drought in both the second and the third year (see Fig. 2.4) probably also caused the larger total numbers of birds observed during these years, as a relative shortage of natural food may have attracted birds usually living outside the study area to the bait food at the banding site.

Most survivorship curves of Regent Bowerbird age classes show an increase in the percentage of individuals known to be alive 29 and 30 months after banding (see Figs 5.1-5.3). Thus, the survival rates of birds banded in the first two months of this study were particularly high. The lower percentage of individuals known to be alive among the birds banded later could have been caused by dispersing or migrating individuals which were seen in the study area for a short period of time only. Movements out of the study area would cause an underestimate of survival rates, so survivorship may be even higher than estimated.

The number of banded Regent Bowerbirds which were observed outside the Sarabah Range study area (Table 5.4) or away from any of the other banding locations (ABBBS microfiches) was, however, only small. Satin Bowerbirds, by contrast, have frequently been re-trapped away from their banding location (e.g. ANON. 1969a, 1976, 1979a,b, 1986, 1992), the furthest distance being 68 km (ANON. 1992). Such long-distance re-traps could indicate a difference in the patterns of movements between the two species, or merely a difference in the ease of trapping.

Satin Bowerbirds have been observed to forage in mixed flocks with Pied Currawongs *Strepera graculina* during the winter months (VELLENGA 1966). Regent Bowerbirds in the Sarabah Range have occasionally joined such mixed species feeding flocks of Satin Bowerbirds and Pied Currawongs, but the movements of these flocks could not be followed. Observations of Regent Bowerbirds in drier, more open habitats and in areas of lower altitude, where the species does not occur during mating and breeding seasons, suggest some local nomadism or short-distance altitudinal migration (ROBERTS 1979; MORRIS et al. 1981; BLAKERS et al. 1984; STORR 1984). The network of ornithologists and bird banders has not yet been extensive enough to follow the movements of individual Regent Bowerbirds.

At present, dispersal and migration do not seem to be important demographic processes in Regent Bowerbirds. The species appears to be largely sedentary. The data do not show sex differences in the patterns of movements. But the fact that none of the banded adult males was ever observed away from its banding location may be of significance; it may indicate a strong faithfulness to a home range and/or a display site. Moreover, adult males had the highest mean annual survival rate of all age classes (Table 5.2).

Operational sex ratio

Estimating the operational sex ratio of a population of Regent Bowerbirds is made difficult by the uncertain status of subadult males. The large testis measurements of some subadult males (Fig. 5.4) suggest that they may be capable of producing sperm.

In Satin Bowerbirds, MARSHALL (1954) found that males can achieve spermatogenesis before they have grown a single blue feather of the adult plumage. VELLENGA (1980a) observed a fifth-year subadult male Satin Bowerbird mating at his bower. Mountings and, in captivity, even successful reproduction by unplumed males have been observed in polygynous bird of paradise species (GILLIARD 1969; LECROY 1981; LASKA et al. 1992). However, such observations of mating unplumed males are very rare. Unplumed males may have reproductive success in exceptional circumstances, for example, in captivity or where fully-plumed males have been removed from a population through hunting (HEALEY 1978; LASKA et al. 1992). Subadult males may have reached sexual maturity physiologically, but behavioural constraints usually prevent reproductive success. Therefore, an estimate based on the percentage of adult males, rather than all sexually active males, in the population should produce a realistic estimate of the operational sex ratio.

A general difficulty in estimating the operational sex ratio of a population is how to consider the time which males and females actually spend searching or competing for mates. Females may be fertilizable for only a brief period, and some males may be sexually active for only part of a mating season. Therefore, SUTHERLAND (1987) defined the operational sex ratio as the ratio of seeking males to seeking females. WILKINSON (1987), however, stressed that the search time which individuals devote to activities related to mating may be impractical to estimate in all but a few taxa. An estimate based on the percentages of adult males and of females which are old enough to breed does not take into consideration the time which individuals devote to mating activities. Nevertheless, such an estimate can indicate whether or not there is a skew in the operational sex ratio.

The estimated female-biased operational sex ratio of about two fertilizable female Regent Bowerbirds to one adult male indicates the potential for individual males to mate with several females. As the absolute sex ratio of the population was nearly balanced (Table 5.1), the skew in the operational sex ratio was largely the result of delayed maturity in male Regent Bowerbirds. Comparable data of populations of other bowerbird species are lacking, but delayed maturity is known in males of other bowerbirds (VELLENGA 1980a; COLLIS & BORGIA 1993; C.B. FRITH & D.W. FRITH in litt.).

WILEY (1974) suggested that sex differences in age at first reproduction may be an important factor in the evolution of non-monogamous mating systems. In contrast, WITTENBERGER (1978) proposed that delayed maturity in males evolves as a response to the patterns of sexual selection found in species with non-monogamous mating systems. PARTRIDGE & ENDLER (1987, pp. 267-268) pointed out that demographic differences between the sexes are "one of the areas where sexual selection can be both cause and effect of life history variation". In species where sexually selected traits, such as large body size, fighting ability and display ability, require time and/or experience to develop, sex differences in age at first reproduction are likely to be a consequence of sexual selection (PARTRIDGE & ENDLER 1987; BEEHLER & FOSTER 1988; LESSELS 1991).

COLLIS & BORGIA (1992) found that juvenile-plumaged male Satin Bowerbirds which had been treated with testosterone attained full adult plumage with their next annual moult, but age-related differences remained in aggression and social dominance between treated and untreated adult-plumaged males. This suggests that age and experience are important in male-male competition. Thus, male bowerbirds may not benefit from attaining adult plumage early, whereas they may benefit from retaining a cryptic plumage until they reach an age at which chances to have reproductive success are better.

One factor of bowerbird population ecology which may have been important in the evolution of non-monogamous mating systems and of age-related differences among males is the high annual survival rates. These high survival rates may have caused sexual selection through promoting differences in male characteristics, for example, in the ability to build, maintain and display at a bower.

6 Bowers: Construction, Decoration, Site Selection and Spatial Distribution

6.1 Introduction

Males of all non-monogamous bowerbird species construct and decorate specialized courts or bowers for their displays to females (see Chapter 1). Unlike the communal display sites or leks of, for example, some birds of paradise, manakins and grouse, male bowerbirds and their display courts are dispersed (DONAGHEY 1981; PRUETT-JONES & PRUETT-JONES 1982; BORGIA 1986a; DIAMOND 1986b). Thus, female bowerbirds cannot directly compare males and their sexual displays; instead, females have to visit several bowers in order to compare males (BORGIA et al. 1985).

Patterns of female mate choice and male mating success have been studied intensively in the Satin Bowerbird. The distribution of copulations among male Satin Bowerbirds was found to show a strong skew in favour of males with well-constructed and highly-decorated bowers (BORGIA 1985a). Therefore, PRUETT-JONES & PRUETT-JONES (1983) and BORGIA et al. (1985) hypothesized that bowers evolved as 'markers' allowing females to assess the status of individual males (the 'marker hypothesis', see Chapter 1).

Male Regent Bowerbirds build two-walled avenue bowers similar in form to those of Satin Bowerbirds (see Figs 1.2d-e and Plates 6 and 12), and it may be expected that the importance of the bower in the mating system is also similar in both species. However, only very few bowers of Regent Bowerbirds have been found (MARSHALL 1954; GILLIARD 1969; BARDEN 1977), leaving it unclear where and to what extent males of this species build bowers (BORGIA et al. 1985). Several explanations for the apparent rarity of Regent Bowerbird bowers have been proposed:

(1) IREDALE (1950, p. 177) claimed that Regent Bowerbirds build bowers only occasionally, that some bowers "are quite primitive", and suggested that bower building "might be a possibly recent habit" in this species, "as if it were only learning the art".

(2) GILLIARD (1969) claimed that Regent Bowerbirds rarely build bowers and hypothesized that the species is in the process of discarding bower building. He suggested that this process may be caused by interspecific competition among Regent and Satin Bowerbirds, two closely-related and largely sympatric species with similar ecological requirements and similar avenue bowers (GILLIARD l.c.).

(3) MARSHALL (1954) rejected any claims of ornithologists and naturalists that Regent Bowerbirds do not build bowers regularly. Instead, he suggested that the bowers are very difficult to find: bowers are small and built in dense vegetation, bower decorations are few and usually placed within the avenue but not in front of the bower, and bower displays are not as noisy as those of other bowerbird species (MARSHALL l.c.).

Which of these three explanations is most likely to be correct? IREDALE's view that bower building in Regent Bowerbirds might be a recently acquired behaviour implies that it evolved separately from other species building avenue bowers. Consequently, IREDALE (1948, 1950) placed the genus *Sericulus* in a separate subfamily. It appears, however, extremely unlikely that a trait as complex as an avenue bower evolved twice in closely-related species. It is much more likely that building this type of bower has evolved only once and that the three genera building avenue bowers (Table 1.1) form a monophyletic group.

GILLIARD's supposition that interspecific competition between Regent and Satin Bowerbirds may be important received some support from BARDEN (1977), who observed Satin Bowerbirds attending and displaying at Regent Bowerbird bowers, as well as stealing bower sticks and decorations. BARDEN (l.c.) concluded that such interference by Satin Bowerbirds, the larger of the two species, may influence the bower site selection of Regent Bowerbirds. A putative hybrid between the two species may also give evidence of interactions (STRESEMANN 1930; CHISHOLM 1966; DIAMOND 1986b).

However, Regent Bowerbirds have frequently built bowers in aviaries (PHILIPPS 1901-1911; BROWN 1956; BELL 1960, 1970; MARSHALL 1970; SINDEL 1989), even when kept together with Satin Bowerbirds (D.J. SPITTALL pers. comm.). It is unlikely that Regent Bowerbirds show bower-building behaviour more regularly in captivity than in the wild (BELL 1970; MARSHALL 1970). In addition, THRELFO (1985) observed and photographed Regent Bowerbirds copulating in a bower. This suggests that bowers are an integral part of the courtship behaviour of this species and are probably built more frequently than assumed by IREDALE and GILLIARD.

Therefore, MARSHALL's assumption is most likely to be correct: Regent Bowerbirds build bowers regularly, but the bowers are difficult to find. Bowers of the congeneric Flame and Fire-maned Bowerbirds are also found only rarely, although their ranges do not overlap with other species building avenue bowers to the extent found in Regent and Satin Bowerbirds (BELL 1970; MACKAY 1989; COATES 1990). All *Sericulus* species live in dense forests where locating their small bowers is difficult, and where sites suitable for bower construction may be more abundant than in the more open habitats of other bowerbird species (BELL 1970).

Finding as many Regent Bowerbird bowers as possible was one of the main aims of the field work for this study, in order to confirm that the species builds bowers regularly. This chapter provides the first detailed study of the construction and decoration of Regent Bowerbird bowers. This information is required to understand the patterns of interactions at bowers, which are dealt with in the following chapter. Bower characteristics, site selection and spatial distribution shall be analysed and compared with bowers of other species, in particular Satin Bowerbirds.

6.2 Materials and methods

In each of the three years of field work of this study, more than five hundred hours were spent searching for bowers in the Sarabah Range study area. Search time was divided equally for western and eastern parts of the study area (see Chapter 2) over the mating period from September until January. Bowers of both Regent and Satin Bowerbirds were searched for, in order to compare bower site characteristics of the two species. During the three mating seasons studied, 75 Regent Bowerbird bowers and 5 Satin Bowerbird bowers were located in the study area. One Regent Bowerbird bower was built at the position of a previous one, reducing the number of bower locations to 74. Bowers with two complete upright walls were designated as active bowers, and all other bowers were designated as rudimentary bowers. The latter group comprised (a) formerly active bowers that were more or less completely destroyed, and (b) incomplete, elementary bowers that merely consisted of a platform of sticks without upright walls. Some formerly active bowers still showed remnants of upright walls, but it was not always possible to distinguish between destroyed bowers and incomplete ones. Therefore, all bowers not showing complete upright walls were called rudimentary.

The following dimensions were measured of all active bowers: maximum length and width of bower, mean width of both bower walls, mean height of both walls (measured as height above centre of bower platform), mean width of bower avenue (measured 50 mm above platform) and orientation of the bower avenue (measured by a compass). The more westerly bower wall was designated as the west wall, the other was designated as the east wall. The entrances of the avenue were designated as north and south entrance accordingly.

Decorations in Regent Bowerbird bowers were counted daily, those in Satin Bowerbird bowers were counted only once. The sticks of eight destroyed, formerly active Regent Bowerbird bowers and of one average-sized Satin Bowerbird bower were collected, counted, measured and, afterwards, returned to the locations they came from.

During the third field season, bower searches were also conducted in the Green Mountains area in Lamington National Park, approximately 8 km south-south-east of the Sarabah Range study area, where 10 Regent Bowerbird bowers and 13 Satin Bowerbird bowers were located. The additional bower search in the Green Mountains had two aims: (a) to obtain data for a comparison of bower decorations used by Regent Bowerbirds in two areas, and (b) to obtain more data of site characteristics of Satin Bowerbird bowers, as the latter species was more common in the Green Mountains than in the Sarabah Range study area.

At each bower site, 16 environmental variables were measured (see Table 6.1). The same environmental variables were also measured at 100 non-bower sites, randomly distributed over the Sarabah Range study area and located using random coordinates taken from MÜHLENBERG (1989, pp. 208-209). Most of the variables were measured within a 1 m radius from the site centre, an area covering most courtship activities at bowers (see Chapter 7).

Table 6.1. Environmental variables measured at bower sites of Regent and Satin Bowerbirds and at randomly-distributed non-bower sites, used for comparative analyses of the selection of bower sites.
Tab. 6.1. Umweltvariable, die an Laubenplätzen von Gelbnacken- und Seidenlaubenvögeln sowie an mit Zufallskoordinaten bestimmten Geländepunkten ohne Laube gemessen wurden, um die Auswahl von Laubenplätzen zu analysieren.

Mnemonic	Variable	Measuring method [unit]
ASPCT	Aspect of site	Measured by compass [°]
SLOPE	Slope of site	Measured by clinometer [°]
CANHT	Canopy height, distance from ground to top of canopy	Measured by scale of a 400 mm telephoto lens [m]
CANOP	Canopy openness, percentage of open canopy	Determined quantitatively from photographs taken with a 20 mm wide-angle lens [%]
HERBS	Herb and grass cover	Estimated percentage within a 1 m radius from the site centre [%]
SHRUB	Shrub cover	As for HERBS
THICK	Liana-thicket cover	As for HERBS
FLOOR	Forest floor without vegetation cover	As for HERBS
LIANA	Number of lianas	Counted within a 1 m radius from the site centre
SAPLS	Number of saplings	As for LIANA
TREES	Number of trees	As for LIANA
DISTP	Mean distance of phanerophytes	Point-centered-quarter-method of MUELLER-DOMBOIS & ELLENBERG (1974) [cm]
DIAMP	Mean diameter of phanerophytes	As for DISTP [mm]
DISTR	Distance to nearest large tree	Measured with a 50 m measuring tape [m]
DISLG	Distance to nearest fallen log	As for DISTR
DISED	Distance to rainforest edge	As for DISTR

Data of environmental characteristics of bower sites and non-bower sites were used for two comparative analyses: (a) site data of 74 Regent Bowerbird bowers and of 100 non-bower sites in the Sarabah Range were compared to identify factors important in the bower-site selection of Regent Bowerbirds, and (b) site data of 74 Regent Bowerbird bowers and 18 Satin Bowerbird bowers were compared to identify similarities and differences in the bower-site selection of the two species. The data set for the second comparison contained data from the Green Mountains, outside the area where data of non-bower sites had been gathered. Therefore, this second data set could not be compared with the data of non-bower sites.

Differences between environmental characteristics of Regent Bowerbird bowers and non-bower sites, as well as differences between bowers of Regent and Satin Bowerbirds, were analysed in two ways: (a) differences in the means of each variable were tested using Student's *t*-tests, and (b) evidence of separation between the groups of sites was tested using a discriminant function analysis on the SPSS^x statistical package (SPSS INC. 1988). This approach was adopted from PRUETT-JONES & PRUETT-JONES (1982) and JONES (1988). Locations of bowers were plotted on a 1:5000 map. This map was produced from enlargements of maps of the 1:25000 Queensland Topographical Map Series and of the 1:25000 map of Lamington National Park of the Department of Forestry. The dispersion of bower sites was analysed using the nearest-neighbour method of CLARK & EVANS (1954). Nearest-neighbour distances between bowers were determined from the 1:5000 map for each mating season. Only active bowers known to be owned by different individuals were included, as the ownership of most rudimentary bowers could not be established. Where an individual male owned more than one bower in a single mating season, the centre between his bowers was used. The nearest-neighbour distances were taken to calculate the bower density using the formula:

$$m = \frac{1}{4r^2}$$

where m is the density per unit area, and r is the mean distance between nearest neighbours. Values of density and mean distance were then used to calculate the proportionality constant, p, from the formula:

$$p = r^2 m$$

Values of p indicate the departure of the distribution from randomness: $p = 1.154$ indicates uniform, hexagonal distribution; $p = 0.25$ indicates random distribution; $p < 0.25$ indicates clumped distribution (CLARK & EVANS 1954; SOUTHWOOD 1966).

6.3 Results

6.3.1 Construction and decoration of bowers

Bower construction

The numbers of active and rudimentary Regent Bowerbird bowers found in the Sarabah Range during the three mating seasons studied are presented in Table 6.2. Although the number of bowers varied between the three years, the total number of 75 found bowers indicates that Regent Bowerbirds build bowers far more regularly than suggested by the small number of bowers found previously (how the number of found bowers is related to the number of males in the study area is considered in the following chapter, see section 7.3.1).

Table 6.2. Number of Regent Bowerbird bowers found in the Sarabah Range during the three mating seasons studied.
Tab. 6.2. Anzahl der Gelbnacken-Laubenvogel-Lauben, die in der Sarabah-Bergkette während der drei untersuchten Paarungssaisons gefunden wurden.

Season	Active bowers	+ Rudimentary bowers	= Total bowers
1989	5 bowers	+ 4 bowers	= 9 bowers
1990	16 bowers	+ 33 bowers	= 49 bowers
1991	12 bowers	+ 5 bowers	= 17 bowers
Total	33 bowers	+ 42 bowers	= 75 bowers

Of the 75 bowers, 33 were found as active bowers and 42 as rudimentary bowers (Table 6.2). Most of the active bowers were maintained by adult males, only four active bowers were maintained by subadult males with brown plumage and, at least partly, yellow iris and orange bill. Immature males with brown plumage, brown iris and black bill were not observed maintaining active bowers. Immature and subadult males, but no adult males, were observed gathering sticks at elementary bower platforms which never showed any upright walls.

Mean measurements of the 33 active bowers found in the Sarabah Range are given in Table 6.3. In most bowers the base was almost square and only a little longer than wide. The base platform of most bowers did not extend beyond the walls. The two walls of a bower were slightly arched over the avenue and were generally similar in their height and width, though these measurements were rarely exactly identical. The distance between bower walls was wide enough for Regent Bowerbirds to hop through the avenue without touching the walls. Avenues were, however, too narrow for birds to turn around while standing in a bower.

Avenues of Regent Bowerbird bowers had a mean deviation of 37.6° ± 23.2° from a north-south orientation (n = 44 bowers, including formerly active bowers which still showed remnants of the avenue). Satin Bowerbird bowers had a mean deviation of 14.6° ± 14.8° (n = 12 bowers). Bower orientation was significantly less close to north-south in Regent Bowerbirds than in Satin Bowerbirds (Mann-Whitney *U*-test, $n_1 = 44$, $n_2 = 12$, $z = -3.01$, $P < 0.003$).

Data on the sticks of the eight formerly active Regent Bowerbird bowers of which all sticks were counted and measured are summarized in Tables 6.4 and 6.5. The bowers contained from 209 to 686 sticks, with a mean of 432 sticks (Table 6.4). In contrast, the one Satin Bowerbird bower of which all sticks were counted, contained 1674 sticks. If sticks scattered around this bower were included, the Satin Bowerbird bower contained over 2000 sticks.

Table 6.3. Dimensions of Regent Bowerbird bowers found in the Sarabah Range (*n* = 33 active bowers).
Tab. 6.3. Abmessungen von Gelbnacken-Laubenvogel-Lauben, die in der Sarabah-Bergkette gefunden wurden (*n* = 33 als Balzplatz genutzte und unterhaltene Lauben).

Measurement	Mean ± *s.d.*
Maximum length of bower	230.6 mm ± 39.5 mm
Maximum width of bower	202.6 mm ± 20.7 mm
Mean height of bower walls	175.6 mm ± 18.9 mm
Mean width of bower walls	59.5 mm ± 11.9 mm
Mean width of bower avenue	81.1 mm ± 10.0 mm

Table 6.4. Measurements of sticks from eight Regent Bowerbird bowers.
Tab. 6.4. Maße der Stöckchen von acht Gelbnacken-Laubenvogel-Lauben.

Bower No.	Number of sticks	Mean length ± *s.d.* [mm]	Mean diameter ± *s.d.* [mm]	Dry mass of all sticks [g]
31	442	139.6 ± 67.3	2.52 ± 1.11	274
35	486	125.3 ± 72.1	2.20 ± 0.78	145
38	369	155.4 ± 74.5	2.75 ± 1.32	210
42	209	144.8 ± 68.8	2.54 ± 1.09	121
52	333	149.1 ± 58.7	2.28 ± 1.07	121
66	686	137.9 ± 52.4	1.84 ± 0.76	177
67	441	139.5 ± 64.9	2.05 ± 0.96	145
71	488	133.9 ± 62.7	2.63 ± 1.18	264
Mean ± *s.d.*	432 ± 138	139.3 ± 65.0	2.30 ± 1.07	182.1 ± 61.1

The dry mass of all sticks of a Regent Bowerbird bower varied from 121 g to 274 g among the eight bowers measured, with a mean of 182 g (Table 6.4). There was no significant correlation between the number of sticks and the mass of a bower (Spearman's rank correlation, $r_s = 0.590$, $n = 8$, $P = 0.118$). Differences in the specific gravity of sticks may partly account for the variation in bower mass. For example, bower 35 was built in a thicket of *Lantana camara* and 34.8 % of its sticks were broken-off parts of the light branches of this shrub species. The large percentage of *Lantana camara* sticks could explain why bower 35 had a below-average mass despite its above-average number of sticks.

Table 6.5. Comparison of sticks of different length classes used in eight Regent Bowerbird bowers.
Tab. 6.5. Vergleich der Stöckchen verschiedener Längenklassen, die in acht Gelbnacken-Laubenvogel-Lauben verwendet wurden.

Length class	Mean diameter ± *s.d.*	*n*	Percentage
≤ 50 mm	2.80 mm ± 1.14 mm	102	3.0 %
51-100 mm	2.33 mm ± 1.14 mm	994	28.8 %
101-150 mm	2.21 mm ± 1.02 mm	1054	30.5 %
151-200 mm	2.23 mm ± 1.01 mm	743	21.5 %
201-300 mm	2.34 mm ± 1.01 mm	488	14.1 %
> 300 mm	2.75 mm ± 1.16 mm	73	2.1 %
	2.30 mm ± 1.07 mm	3454	100.0 %

Only rarely, however, was it possible to identify the plant species where bower sticks originated from. While most sticks were broken-off parts of branches, some bowers also contained petioles (e.g. the tomentose petioles of *Diploglottis cunninghamii*). Of the 3454 sticks collected from the eight bowers, 2796 (80.9 %) were straight, unbranched and without thorns. Touching bower-sticks were often fused by whitish fungi.

All sticks from the eight bowers were grouped in six length classes, and the mean diameter and frequency of sticks of the six length classes are compared in Table 6.5. Most sticks were medium-sized. The mean diameter of medium-sized sticks was smaller than the mean diameter of shorter and longer sticks.

Differences between the diameters of sticks may be related to the way different sticks were used in bower building. The platform of a bower was predominantly made up of medium-sized, relatively thin sticks. Long sticks of various thickness were mainly used to build bower walls. Short and stout sticks were used at the base of bower walls, presumably to shore up the walls, and at the entrances of a bower avenue, resulting in a smoother surface of the entrances.

With a mean diameter of 2.30 ± 1.07 mm, the 3454 sticks from the eight Regent Bowerbird bowers (Table 6.5) were slightly, but significantly, thicker than the 1674 measured sticks from the Satin Bowerbird bower, which had a mean diameter of 2.22 ± 0.76 mm (Student's *t*-test, $t = 3.076$, $d.f. = 5126$, $P < 0.01$).

Most active bowers already showed upright walls when they were found. Only bower 35 was discovered when a male had just begun building it. This made it possible to observe the process of bower building. The male first constructed the bower platform, using medium-sized sticks. These were placed crossing each other in various directions and were pressed downward by the male with his bill. By means of sideways bill-movements the male made an elongated depression in the middle axis of the platform, the position of the future avenue. After the platform had reached a thickness of approximately 15 mm, the male started building the walls, by inserting longer sticks vertically into the slightly higher parts of the platform, beside the depression. Walls and avenue became increasingly discernible, with more sticks constantly added by the male, working from either entrance or from within the avenue. The shape of the avenue was rounded through adding short sticks.

When the male left the bower to collect a new stick, about every second time he picked up a dry, brown leaf from the forest floor in the immediate vicinity of the bower and dropped the leaf a few metres away. Through this activity, most leaves were removed from the forest floor surrounding the bower; in particular, the ground near the entrances of the avenue was cleaned of old leaves.

All sticks were gathered within a radius of 5 m from the bower. While building the platform, most sticks were picked up from the forest floor, and the male brought up to three sticks simultaneously to the bower. In contrast, during the second phase of bower construction, when the walls were built, the majority of sticks were broken off nearby shrubs and trees and were brought separately to the bower. As a result, the mean time the male required to collect and put in one stick increased from 11.9 ± 5.8 seconds while building the platform (n = 169 sticks) to 37.4 ± 16.1 seconds while building the walls (n = 79 sticks).

It took the male three hours of almost continuous building to construct the complete bower with two upright walls, though the walls were still comparatively flimsy at that stage. On the following day, the male resumed bower building, added more sticks to the walls and painted the walls for the first time. The first visit of a female also took place on the day following the bower construction.

Bower decoration

All 29 active bowers of adult males, and also two of the four active bowers of subadult males, showed paint on the inside of their walls. The decoration objects of Regent Bowerbird bowers were generally found in the avenue. The only exception were objects which had recently been used in a display and had not yet been brought back to the avenue by the bower owner.

The types and numbers of decoration objects of Regent Bowerbird bowers found in the Sarabah Range are presented in Table 6.6. Median numbers of decorations were used to reflect a mixture of objects representative of a bower, as the numbers of objects in a bower often varied slightly from day to day. The median number of decorations in a bower during its period of maintenance ranged from 1 to 23 objects. The mean number of objects was 10.3 ± 5.7 (n = 33 active bowers). The maximum number of objects ever found in a bower was 29. The number of bowers of subadult males was too small to test differences in the number of decoration objects between bowers of adult and subadult males.

Of the decoration objects listed in Table 6.6, 67.4 % were vegetable objects, 19.1 % animal objects and 13.5 % man-made objects (n = 341 decoration objects). The four types of decoration used most regularly in the 33 active bowers found in the Sarabah

Table 6.6. Decoration of Regent Bowerbird bowers found in the Sarabah Range. Figures are median numbers of objects during period of bower maintenance. Bowers 20, 56, 57 and 58 were owned by subadult males, all other bowers were owned by adult males.

Tab. 6.6. Dekoration von Gelbnacken-Laubenvogel-Lauben, die in der Sarabah-Bergkette gefunden wurden. Angegeben werden die Medianwerte an Dekorationsobjekten während des Laubenunterhalts. Die Lauben 20, 56, 57 und 58 gehörten subadulten Männchen, alle übrigen Lauben gehörten adulten Männchen.

Type of bower decoration	Bower number																																
	1	2	3	4	5	10	15	20	31	32	35	38	42	46	50	52	54	55	56	57	58	59	61	62	64	65	66	67	68	70	71	72	74
Vegetable objects:	15	4	12	7	11	8	9	3	7	4	17	17	9	4	6	8	5	6	3	21	5	1	6	1	6	2	3	6	4	5	7	4	4
Green leaves	10	4	12	3	9	6	7	1	5	3	7	5	1	2	3	2	1	4	2	1	4	1	3	1	5	0	0	4	3	0	5	1	1
Petals	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Deep Yellow-wood fruit	4	0	0	3	2	2	2	2	1	1	6	12	4	2	3	6	4	2	0	19	1	0	3	0	1	2	2	2	1	4	2	3	3
Other fruit	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
Black Apple seeds	0	0	0	0	0	0	0	0	1	0	3	0	4	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Animal objects:	0	8	6	7	2	2	1	0	1	2	1	5	3	1	3	0	3	0	1	1	3	1	1	0	0	1	1	1	2	3	2	1	2
Snail shells	0	6	3	7	1	2	1	0	1	2	1	3	3	1	3	0	3	0	0	1	0	1	1	0	0	1	1	1	2	3	1	1	2
Cicada exuviae	0	0	3	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	0	0	1	0	0
Other exuviae	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Man-made objects:	2	8	0	2	0	0	2	0	4	3	1	1	1	2	5	0	1	0	0	0	1	0	1	0	0	1	4	1	1	2	2	0	1
Pieces of blue plastic	2	8	0	2	0	0	2	0	4	3	1	1	1	2	5	0	1	0	0	0	1	0	1	0	0	1	3	1	1	2	2	0	1
Other man-made objects	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Total	17	20	18	16	13	10	12	3	12	9	19	23	13	7	14	8	9	6	4	22	9	2	8	1	6	4	8	8	7	10	11	5	7

Range were: green leaves (in 30 bowers), fruit of Deep Yellow-wood *Rhodosphaera rhodanthema* trees (in 28 bowers), snail shells (in 25 bowers) and pieces of blue plastic (in 21 bowers). All other decoration types were found in less than 20 % of the bowers. Most green leaves found in bowers were fresh and soft. Old and dry leaves were regularly replaced by bower owners. Deep Yellow-wood fruit are globose drupes, 8-10 mm in diameter, consisting of a papery, brown and shining epicarp and a thick, woody endocarp. They are produced in large panicles, up to 20 cm long and 10 cm wide, each panicle carrying several dozen drupes (see STANLEY & ROSS 1983; WILLIAMS et al. 1984). The drupes dry and remain on trees for many months. Deep Yellow-wood trees were abundant in the study area (see Appendix 1) and carried an abundance of fruit in each of the three field seasons of this study.

Seeds of Black Apple *Planchonella australis* trees are, with their brown colour and shining surface, superficially somewhat similar to Deep Yellow-wood fruit. Black Apple trees fruited only in the second of the three field seasons of this study, and only during that year were their seeds found in Regent Bowerbird bowers.

Snail shells were by far the most common animal objects found in bowers. The snail shells used as bower decoration were brown, shiny and 10-20 mm in diameter. All except one of the man-made objects were pieces of dark blue plastic (Table 6.6). The remaining object was a piece of golden foil.

Decoration objects of Regent Bowerbird bowers found in the Green Mountains are summarized in Table 6.7. The general pattern of bower decoration was similar to bowers found in the Sarabah Range study area. The majority of the decoration objects were vegetable objects, predominantly green leaves. Most of the animal objects were snail shells, and most of the man-made objects were pieces of blue plastic.

There were, however, no Deep Yellow-wood drupes in the Green Mountains bowers. The nearest trees of this species were found 6 km north of this area. The species of fruit found most regularly as bower decoration were the dark purplish drupes of Saffron-heart *Halfordia kendack* trees (in 3 of 6 bowers). In the Green Mountains, no single fruit species appeared to be as common as bower decoration as fruit of the Deep Yellow-wood was in the Sarabah Range study area.

6.3.2 Site selection and spatial distribution of bowers

Bower site selection

The means of the environmental data of 74 Regent Bowerbird bower sites and 100 non-bower sites are given in Table 6.8, together with the results of Student's *t*-tests on differences between means of the two groups. Highly significant differences (at the level $P < 0.001$) were found in eight of the 16 variables measured.

The results of the discriminant function analysis for the 174 sampled sites are given in Table 6.9. The single canonical discriminant function derived from the analysis was highly significant (eigenvalue = 1.511, Wilks' Lambda = 0.3982, χ^2 = 151.48, *d.f.* =

Table 6.7. Decoration of Regent Bowerbird bowers found in the Green Mountains. Figures are median numbers of objects during period of bower maintenance. All bowers were owned by adult males.
Tab. 6.7. Dekoration von Gelbnacken-Laubenvogel-Lauben, die in den Green Mountains gefunden wurden. Angegeben werden die Medianwerte an Dekorationsobjekten während des Laubenunterhalts. Alle Lauben gehörten adulten Männchen.

Type of bower	Bower number					
decoration	2	3	5	6	9	10
Vegetable objects:	3	10	1	9	9	12
Green leaves	2	6	1	5	6	9
Saffron-heart fruit	1	3	0	2	0	0
Other fruit	0	1	0	1	2	3
Brown seeds	0	0	0	1	1	0
Animal objects:	2	5	2	8	4	5
Snail shells	2	5	0	6	2	5
Cicada exuviae	0	0	1	2	2	0
Other exuviae	0	0	1	0	0	0
Man-made objects:	2	1	1	1	3	4
Pieces of blue plastic	1	1	1	0	3	3
Other man-made objects	1	0	0	1	0	1
Total	7	16	4	18	16	21

15, $P < 0.0001$). A classification procedure correctly predicted the group membership of 157 of the 174 sites (90.2 %); correctly classified were 63 of the 74 bower sites (85.1 %) and 94 of the 100 non-bower sites (94.0 %). This clear evidence of separation between bower sites and non-bower sites indicates that certain environmental factors were very important in the bower site selection by male Regent Bowerbirds.

The contribution of each variable to the discrimination between bower sites and non-bower sites was evaluated through testing Wilks' Lambda values for all variables using univariate *F*-ratios. The data in Table 6.9 show that seven variables were of particular importance in distinguishing between the two groups ($P < 0.0001$): LIANA, THICK, FLOOR, CANHT, CANOP, SLOPE and DISTP. The first five of these seven discriminating variables were most highly correlated with the discriminant function ($r > 0.35$) and were the most important predictors of discrimination among groups. This indicates that the following five environmental factors were most important in the bower site selection by Regent Bowerbirds: number of lianas (LIANA), percentage of liana-thicket cover (THICK), percentage of open forest floor (FLOOR), canopy height (CANHT) and canopy openness (CANOP).

The group means in Table 6.8 reveal that, compared with randomly located non-bower sites, the Regent Bowerbird bower sites were characterized by a larger number of lianas,

Table 6.8. Student's *t*-tests for environmental variables of Regent Bowerbird bower sites and non-bower sites. Variables are listed in order of significance of *t*-tests, mnemonics are defined in Table 6.1.

Tab. 6.8. Students *t*-Tests für Umweltvariable von Gelbnacken-Laubenvogel-Laubenplätzen und von Geländepunkten ohne Laube. Die Variablen werden in der Reihenfolge der Signifikanz der *t*-Tests aufgeführt, die Abkürzungen werden in Tab. 6.1 erklärt.

Variable	Bower sites (n = 74)	Non-bower sites (n = 100)	t	P
LIANA	36.57 ± 21.26	7.25 ± 7.22	12.84	***
THICK	44.69 ± 20.32	26.92 ± 16.96	11.89	***
FLOOR	47.47 ± 18.56	70.31 ± 19.52	-7.79	***
CANHT	10.76 ± 3.45	14.30 ± 3.91	-6.21	***
CANOP	24.12 ± 11.21	16.52 ± 6.27	5.68	***
SLOPE	12.82 ± 5.05	16.67 ± 5.84	-4.56	***
DISTP	146.40 ± 91.88	103.08 ± 46.09	4.08	***
HERBS	2.23 ± 6.40	8.00 ± 13.43	-3.42	***
DISED	94.61 ± 80.82	125.60 ± 91.71	-2.32	*
SHRUB	5.61 ± 6.89	7.92 ± 6.95	-2.18	*
DISLG	3.31 ± 3.30	4.40 ± 3.38	-2.13	*
DISTR	10.61 ± 6.26	8.95 ± 5.29	1.89	*n.s.*
DIAMP	50.88 ± 33.79	44.22 ± 37.06	1.22	*n.s.*
TREES	0.28 ± 0.65	0.37 ± 0.54	-0.95	*n.s.*
SAPLS	3.76 ± 3.34	4.06 ± 3.12	-0.62	*n.s.*
ASPCT	158.72 ± 109.72	153.68 ± 94.33	0.33	*n.s.*

a higher percentage of liana-thicket cover, a lower percentage of open forest floor, a lower canopy height, and a higher percentage of open canopy. Of these five factors, the first three were clearly interrelated: the percentage of liana-thicket cover was highly significantly correlated with the number of lianas (r = 0.725, $P < 0.001$) and inversely correlated with the percentage of open forest floor (r = - 0.737, $P < 0.001$). These three factors, nevertheless, express different aspects of the environment of a particular site; for example, a site with a high percentage of liana-thicket cover could still have a relatively small number of lianas if these were particularly thick. The group means of the remaining two of the five most important environmental factors indicate that male Regent Bowerbirds frequently selected sites for bower building in secondary regrowth, with a comparatively low and more open canopy.

Bower sites also differed from non-bower sites in being on less steep slopes, in having a larger mean distance to the nearest phanerophytes (trees or shrubs), and in having a lower percentage of herb and grass cover. The group means for these three variables were highly significantly different (see SLOPE, DISTP and HERBS in Table 6.8), but the three variables were less important in discriminating between bower sites and non-bower sites.

Table 6.9. Discriminant function analysis for environmental variables of Regent Bowerbird bower sites and non-bower sites. Wilks' Lambda statistics (*U*-statistic), univariate *F*-ratio and pooled within-groups correlations between discriminating variables (predictors) and canonical discriminant function. Variables are ordered by size of correlation within function, mnemonics are defined in Table 6.1.

Tab. 6.9. Diskriminanzanalyse von Umweltvariablen von Gelbnacken-Laubenvogel-Laubenplätzen und von Geländepunkten ohne Laube. Wilks' Lambda (*U*-Statistik), univariate *F*-Werte und gepoolte Innergruppen-Korrelation zwischen diskriminierenden Variablen (Prädiktoren) und kanonischer Diskriminanzfunktion. Die Variablen werden in der Reihenfolge ihrer diskriminatorischen Bedeutung aufgeführt, die Abkürzungen werden in Tab. 6.1 erklärt.

Variable	Wilks' Lambda	*F*	*P*	Pooled within-groups correlations between discriminating variables and canonical discriminant function
LIANA	0.5108	164.7	< 0.0001***	0.79606
THICK	0.5491	141.3	< 0.0001***	0.73715
FLOOR	0.7392	60.67	< 0.0001***	-0.48309
CANHT	0.8313	34.91	< 0.0001***	-0.36646
CANOP	0.8422	32.22	< 0.0001***	0.35206
SLOPE	0.8933	20.55	< 0.0001***	-0.28115
DISTP	0.9055	17.94	< 0.0001***	0.26271
HERBS	0.9364	11.69	0.0008***	-0.21201
DISED	0.9697	5.373	0.0216*	-0.14377
SHRUB	0.9732	4.741	0.0308*	-0.13504
DISLG	0.9741	4.571	0.0339*	-0.13260
DIAMP	0.9758	4.258	0.0406*	0.12798
DISTR	0.9776	3.938	0.0488*	0.12307
TREES	0.9948	0.9010	0.3439	-0.05887
SAPLS	0.9978	0.3789	0.5390	-0.03818
ASPCT	0.9994	0.1057	0.7455	0.02017

The comparison of environmental variables of the 74 Regent Bowerbird bower sites and 18 Satin Bowerbird bower sites revealed highly significant differences between group means in five of the 16 variables measured (see Table 6.10). The canonical discriminant function derived from the discriminant function analysis for the 92 bower sites of the two species was also highly significant (eigenvalue = 1.151, Wilks' Lambda = 0.4649, $\chi^2 = 63.19$, *d.f.* = 15, $P < 0.0001$). A classification procedure correctly predicted the group membership of 86 of the 92 sites (93.5 %); correctly classified were 68 of the 74 bower sites of Regent Bowerbirds (91.9 %) and all 18 bower sites of Satin Bowerbirds. This indicates a very clear separation between bower sites of the two species.

The results of the discriminant function analysis in Table 6.11 show that five variables were of particular importance in distinguishing between the two groups: THICK, LIANA, SHRUB, HERBS and DISED. These five variables were most highly correlated

Table 6.10. Student's *t*-tests for environmental variables of bower sites of Regent and Satin Bowerbirds. Variables are listed in order of significance of *t*-tests, mnemonics are defined in Table 6.1.
Tab. 6.10. Students *t*-Tests für Umweltvariable von Laubenplätzen von Gelbnacken- und Seidenlaubenvögeln. Die Variablen werden in der Reihenfolge der Signifikanz der *t*-Tests aufgeführt, die Abkürzungen werden in Tab. 6.1 erklärt.

Variable	Regent Bowerbird bowers (n = 74)	Satin Bowerbird bowers (n = 18)	t	P
THICK	44.69 ± 20.32	18.39 ± 12.08	5.26	***
LIANA	36.57 ± 21.26	11.44 ± 11.01	4.84	***
SHRUB	5.61 ± 6.89	14.72 ± 10.87	-4.45	***
HERBS	2.23 ± 6.40	12.78 ± 17.40	-4.22	***
DISED	94.61 ± 80.82	14.91 ± 22.72	4.13	***
CANHT	10.76 ± 3.45	8.19 ± 2.99	2.90	**
SLOPE	12.82 ± 5.05	9.61 ± 5.15	2.41	*
DIAMP	50.88 ± 33.79	36.68 ± 25.61	1.67	*n.s.*
ASPCT	158.72 ± 109.72	116.25 ± 93.01	1.51	*n.s.*
FLOOR	47.47 ± 18.56	54.11 ± 12.88	-1.43	*n.s.*
SAPLS	3.76 ± 3.34	2.67 ± 2.38	1.30	*n.s.*
DISLG	3.31 ± 3.30	3.80 ± 3.92	-0.55	*n.s.*
CANOP	24.12 ± 11.21	25.82 ± 16.19	-0.53	*n.s.*
DISTR	10.61 ± 6.26	11.48 ± 7.35	-0.51	*n.s.*
DISTP	146.40 ± 91.88	136.90 ± 58.72	0.42	*n.s.*
TREES	0.28 ± 0.65	0.22 ± 0.43	0.38	*n.s.*

with the discriminant function ($r > 0.4$). This indicates that the bower site selection by Regent and Satin Bowerbirds is mainly different in the following five environmental factors: percentage of liana-thicket cover (THICK), number of lianas (LIANA), shrub cover (SHRUB), herb and grass cover (HERBS) and distance to rainforest edge (DISED). The group means in Table 6.10 reveal that, compared with Satin Bowerbird bower sites, the Regent Bowerbird bower sites were characterized by a higher percentage of liana-thicket cover, a larger number of lianas, a lower percentage of shrub cover, a lower percentage of herb and grass cover, and a larger distance to the edge of the rainforest. The percentage of liana-thicket cover was, again, highly significantly correlated with the number of lianas ($r = 0.724$, $P < 0.001$).

Bower sites of both Regent and Satin Bowerbirds consisted of about 50 % forest floor without vegetation cover (see FLOOR data in Table 6.10). The composition of the vegetation on the other 50 % of the sites was, however, different: liana thickets were very characteristic of bower sites of Regent Bowerbirds (see Plate 27), whereas bower sites of Satin Bowerbirds showed a mixture of shrubs, herb and grass cover, and lianas. The clear evidence that Satin Bowerbird bowers were located much closer to the rainforest edge than Regent Bowerbird bowers (see DISED data in Table 6.10) is important for considerations of interactions and competition between the two species.

Table 6.11. Discriminant function analysis for environmental variables of bower sites of Regent and Satin Bowerbirds. Wilks' Lambda statistics (*U*-statistic), univariate *F*-ratio and pooled within-groups correlations between discriminating variables (predictors) and canonical discriminant function. Variables are ordered by size of correlation within function, mnemonics are defined in Table 6.1.

Tab. 6.11. Diskriminanzanalyse von Umweltvariablen von Laubenplätzen von Gelbnacken- und Seidenlaubenvögeln. Wilks' Lambda (*U*-Statistik), univariate *F*-Werte und gepoolte Innergruppen-Korrelation zwischen diskriminierenden Variablen (Prädiktoren) und kanonischer Diskriminanzfunktion. Die Variablen werden in der Reihenfolge ihrer diskriminatorischen Bedeutung aufgeführt, die Abkürzungen werden in Tab. 6.1 erklärt.

Variable	Wilks' Lambda	*F*	*P*	Pooled within-groups correlations between discriminating variables and canonical discriminant function
THICK	0.7651	27.64	< 0.0001***	0.51654
LIANA	0.7932	23.46	< 0.0001***	0.47588
SHRUB	0.8197	19.79	< 0.0001***	-0.43711
HERBS	0.8348	17.81	0.0001***	-0.41466
DISED	0.8408	17.04	0.0001***	0.40565
CANHT	0.9147	8.394	0.0047**	0.28467
SLOPE	0.9396	5.784	0.0182*	0.23631
DIAMP	0.9700	2.780	0.0989	0.16383
ASPCT	0.9752	2.291	0.1336	0.14871
FLOOR	0.9777	2.053	0.1554	-0.14078
SAPLS	0.9814	1.702	0.1953	0.12819
DISTR	0.9955	0.4094	0.5239	-0.06287
DISLG	0.9967	0.2940	0.5890	-0.05328
CANOP	0.9969	0.2783	0.5991	-0.05184
DISTP	0.9981	0.1742	0.6774	0.04101
TREES	0.9984	0.1446	0.7046	0.03736

Spatial distribution of bowers

The spatial distribution of Regent Bowerbird bowers in the Sarabah Range study area is shown in Figures 6.1 to 6.3 for the three mating seasons studied. Of the total of 75 located bowers, 65 bowers (86.7 %) were situated more than 650 m above sea level, close to the ridgetop. The rainforest area in which bowers were searched covered an area of 186.3 ha (see Chapter 2), of which 70.3 ha (37.7 %) were situated more than 650 m above sea level. Therefore, Regent Bowerbirds selected sites for bower building highly significantly more often above 650 m than below this elevation ($\chi^2 = 51.27$, *d.f.* = 1, $P < 0.00001$).

Mean nearest-neighbour distances between bower sites were 330.6 ± 85.1 m in 1989 ($n = 4$), 155.2 ± 105.6 m in 1990 ($n = 12$), and 188.1 ± 85.8 m in 1991 ($n = 8$). The pooled mean for the three mating seasons studied was 195.4 ± 112.1 m ($n = 24$).

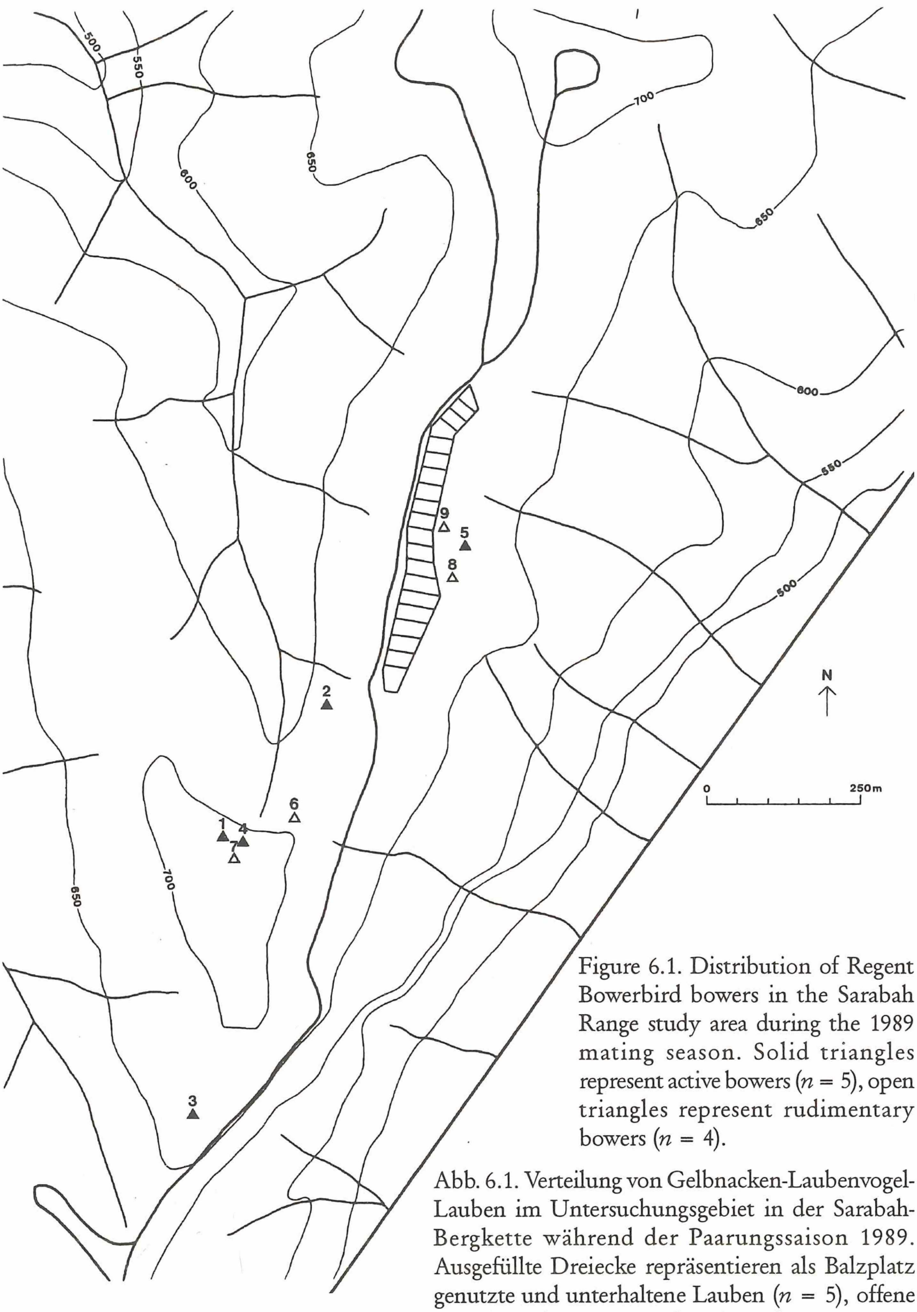

Figure 6.1. Distribution of Regent Bowerbird bowers in the Sarabah Range study area during the 1989 mating season. Solid triangles represent active bowers ($n = 5$), open triangles represent rudimentary bowers ($n = 4$).

Abb. 6.1. Verteilung von Gelbnacken-Laubenvogel-Lauben im Untersuchungsgebiet in der Sarabah-Bergkette während der Paarungssaison 1989. Ausgefüllte Dreiecke repräsentieren als Balzplatz genutzte und unterhaltene Lauben ($n = 5$), offene Dreiecke rudimentäre Lauben ($n = 4$).

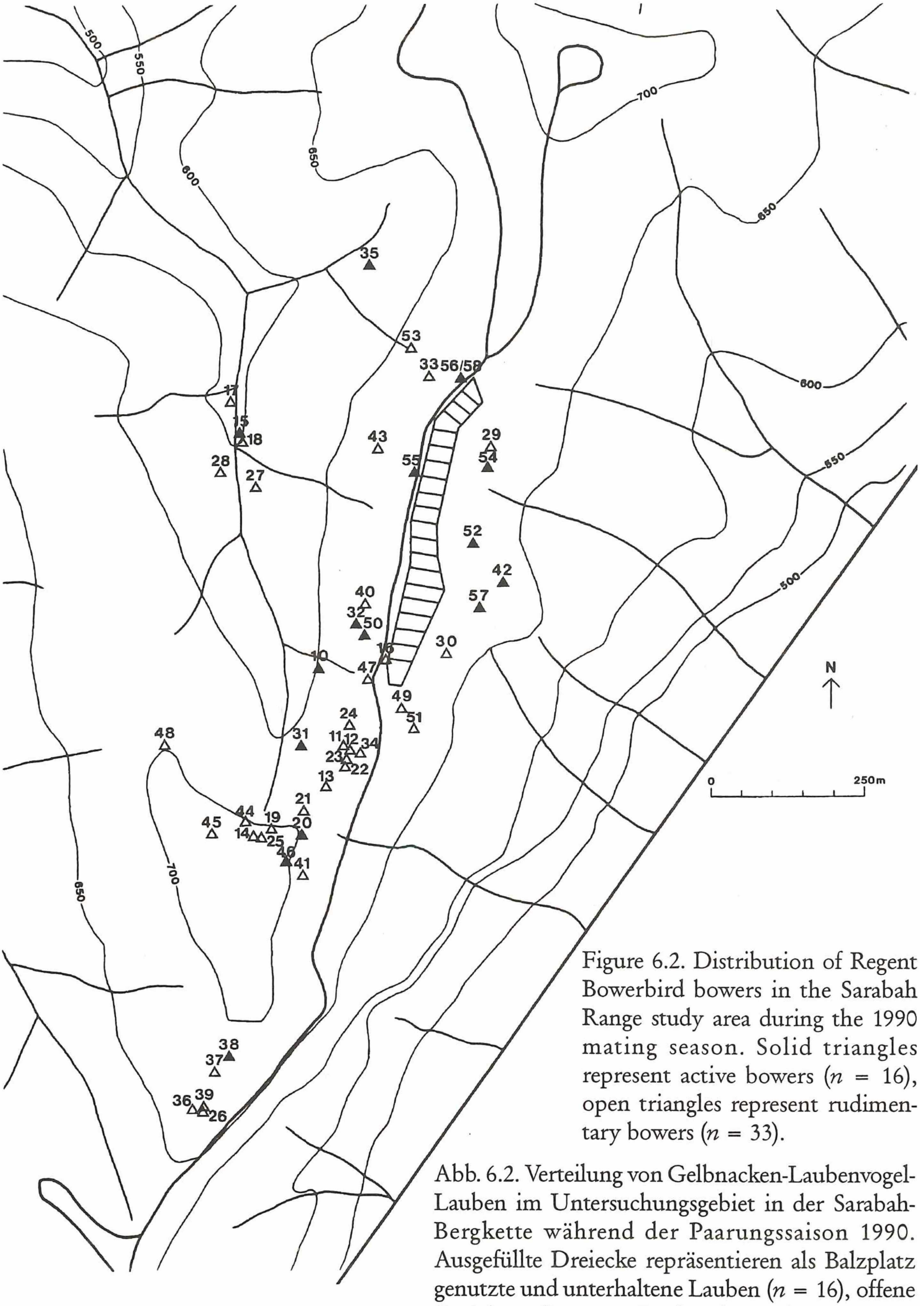

Figure 6.2. Distribution of Regent Bowerbird bowers in the Sarabah Range study area during the 1990 mating season. Solid triangles represent active bowers (*n* = 16), open triangles represent rudimentary bowers (*n* = 33).

Abb. 6.2. Verteilung von Gelbnacken-Laubenvogel-Lauben im Untersuchungsgebiet in der Sarabah-Bergkette während der Paarungssaison 1990. Ausgefüllte Dreiecke repräsentieren als Balzplatz genutzte und unterhaltene Lauben (*n* = 16), offene Dreiecke rudimentäre Lauben (*n* = 33).

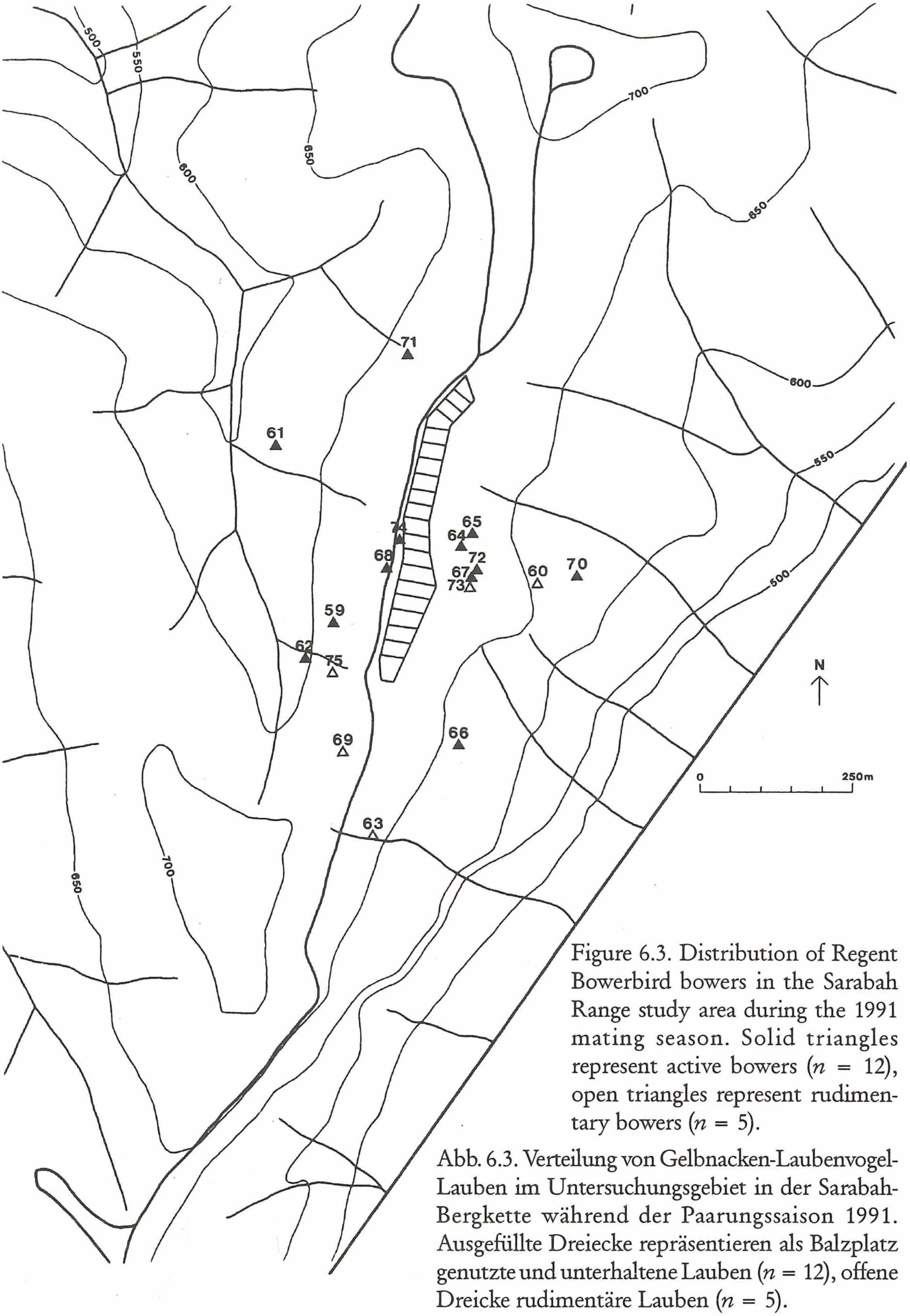

Figure 6.3. Distribution of Regent Bowerbird bowers in the Sarabah Range study area during the 1991 mating season. Solid triangles represent active bowers (*n* = 12), open triangles represent rudimentary bowers (*n* = 5).

Abb. 6.3. Verteilung von Gelbnacken-Laubenvogel-Lauben im Untersuchungsgebiet in der Sarabah-Bergkette während der Paarungssaison 1991. Ausgefüllte Dreiecke repräsentieren als Balzplatz genutzte und unterhaltene Lauben (*n* = 12), offene Dreicke rudimentäre Lauben (*n* = 5).

The values of the proportionality constant, p, calculated from these mean nearest-neighbour distances between bower sites and the densities of active bowers in the searched rainforest area of 186.3 ha were 0.235 in 1989, 0.155 in 1990 and 0.152 in 1991, indicating that Regent Bowerbird bowers were concentrated in parts of the study area ($p < 0.25$). The bowers were found in an area covering just 44.4 ha or 23.8 % of the searched rainforest area. Values of p within this area of 44.4 ha were 0.985 in 1989, 0.651 in 1990 and 0.638 in 1991. This indicates that, while Regent Bowerbird bowers were found only in less than a quarter of the rainforest area studied, the bowers were widely spaced ($p \gg 0.25$) in the area which Regent Bowerbird males used for bower building: along the ridgetop of the Sarabah Range (see Figs 6.1-6.3).

6.4 Discussion

Construction and decoration of bowers

The total of 75 Regent Bowerbird bowers found in the Sarabah Range study area during the three mating seasons studied (Table 6.2) far exceeds the total number of bowers previously described in the literature. This evidence strongly supports the assumption of MARSHALL (1954) that Regent Bowerbirds build bowers regularly, but the bowers are very difficult to find.

The few bowers that have been found previously were mostly discovered by chance, not as a result of extensive searches (e.g. RAMSAY 1867; JACKSON 1920; PLOMLEY 1935; GODDARD 1947). For decades, "eggs, not bowers, have been the quarry of most observers" (MARSHALL 1954, p. 112). Wildlife photographers, on the other hand, have found bowers quite often (BREEDEN & BREEDEN 1972; CHAFFER 1984 and in litt.; THRELFO 1985 and pers. comm.; H. BESTE & J. BESTE pers. comm.).

Most recent studies on the reproductive biology and evolutionary ecology of bowerbirds focused on species with much larger bowers, which are comparatively easy to find. The failure of some recent attempts to find Regent Bowerbird bowers regularly in the wild (BARDEN 1977; G. BORGIA & R.H. DONAGHEY pers. comm.) only stresses the difficulty in discovering them in dense vegetation, but should not lead to continued suppositions that the species builds bowers only rarely or occasionally.

The bowers of Regent Bowerbirds have been described as "primitive" (IREDALE 1950, p. 177), "poorly made" (BELL 1970, p. 67) and "much less elaborately constructed" than those of other species (COOPER & FORSHAW 1977, p. 260). In contrast, some bowers have been described as having "a very pretty appearance" (RAMSAY 1867, p. 457), "perfect", though only small (CAMPBELL 1900, p. 210), or as "well-built, tidy, and firm structure" (CHAFFER 1984, p. 46).

The data on the Sarabah Range bowers make it possible, for the first time, to examine the range of bower constructions and decoration objects within a population. As discernible from the variation in the number of sticks in Regent Bowerbird bowers

(Table 6.4), some bowers were quite flimsy with only about 200 sticks, whereas others were substantial constructions of up to 700 sticks. Thus, bowers showed the range of construction levels (see Plates 28-30) reflected in the above quotations. A similar variation occurred in the number of decoration objects (Tables 6.6-6.7).

Compared to the bowers of other species (see Table 6.12), Regent Bowerbird bowers have much smaller dimensions, consist of a much smaller number of sticks and are decorated with a much smaller number of objects. The range of bower dimensions and decoration numbers is also considerably smaller than in bowers of other species. Only the bowers of Flame and Fire-maned Bowerbirds, the other species in the genus *Sericulus*, are similar to Regent Bowerbird bowers.

Bowers of larger species are generally larger than those of smaller species, but the differences in bower dimensions and in numbers of decoration objects by far exceed the size differences among bowerbird species. In the Fawn-breasted Bowerbird *Chlamydera cerviniventris*, the number of decorations is relatively small, but the species constructs some of the largest display sites of all bowerbirds.

If well-constructed and highly-decorated bowers were as important in the mating behaviour of *Sericulus* species as in other bowerbirds (see BORGIA 1985a; BORGIA & MUELLER 1992), sexual selection should favour males which collect more sticks and more decoration objects for their bowers. The fact that the dimensions and decoration numbers of *Sericulus* bowers are always small could be due to (a) limited bower-building resources or (b) due to differences in the function of the bower in the mating system between *Sericulus* species and other bowerbird genera.

All *Sericulus* species are found in tropical to subtropical closed forests (see Chapter 3) where a limited supply of both sticks suitable for bower building and objects suitable for bower decoration seems extremely unlikely. However, in other bowerbird genera it was found that certain types of bower decoration, which are rare in the birds' habitat, are of particular importance for the mating success of bower-owning males. For example, male Satin Bowerbirds use feathers of two parrot species, the Crimson Rosella *Platycercus elegans* and the Eastern Rosella *P. eximius*, as decoration objects (see Plate 6) and steal them from bowers of other males (VELLENGA 1970; BORGIA 1986a; BORGIA & GORE 1986). Males of Archbold's Bowerbird use the rare plume feathers of male King of Saxony Birds of Paradise *Pteridophora alberti* as bower decoration (FRITH & FRITH 1990b; FRITH et al. 1996; see Plate 4). In contrast, feathers have never been found in any bowers of *Sericulus* species (MARSHALL 1954; GILLIARD 1969; BARDEN 1977; MACKAY 1989; COATES 1990; this study).

Among the types of decoration found regularly in Regent Bowerbird bowers (Tables 6.6-6.7), snail shells, cicada exuviae and pieces of blue plastic could represent relatively rare objects. However, snail shells and cicada exuviae were regularly found during field work, and it appeared that male Regent Bowerbirds did not gather as many of these objects as availability would permit. While natural blue objects can probably be considered as rare, an abundance of pieces of blue plastic was found in the bowers of

Table 6.12. Interspecific comparison of avenue bowers (Regent Bowerbird highlighted in bold). In all species except the Fawn-breasted Bowerbird, the measurements of bower length and width refer to the dimensions of bower walls, not to the maximum platform extension. In the Fawn-breasted Bowerbird, measurements include the platform.

Tab. 6.12. Interspezifischer Vergleich von Alleelauben (Regent Bowerbird bzw. Gelbnacken-Laubenvogel durch Fettdruck hervorgehoben). Bei allen Arten außer dem Fawn-breasted Bowerbird bzw. Braunbauch-Laubenvogel beziehen sich die Maße von Laubenlänge und -breite auf die Laubenwände und nicht auf die maximale Ausdehnung der Laubenplattform. Beim Braunbauch-Laubenvogel schließen die Maße die Plattform mit ein.

Bowerbird species	Total length of male bird	Length of bower	Width of bower	Number of sticks	Number of decorations	References
Genus *Sericulus*:						
Flame Bowerbird - *aureus**	25.5 cm	c. 18 cm	?	?	5-6	1,2
Flame Bowerbird - *ardens***	24.5 cm	c. 23 cm	c. 16 cm	?	2-10	2,3
Fire-maned Bowerbird	26.5 cm	c. 20 cm	c. 18 cm	?	8	2,4
Regent Bowerbird	**25-28 cm**	**19-27 cm**	**18-22 cm**	**209-686**	**1-29**	**5**
Genus *Ptilonorhynchus*:						
Satin Bowerbird	27-30 cm	19-41 cm	21-39 cm	>2000	36 - >200	1,5,6,7,8,9
Genus *Chlamydera*:						
Western Bowerbird	28-31 cm	c. 55 cm	c. 57 cm	?	up to >1600	8,10,11
Spotted Bowerbird	28-31 cm	35-70 cm	47-74 cm	?	100 - >1400	9,12,13,14
Great Bowerbird	34-36 cm	44-69 cm	56-60 cm	4000-5000	100 - >2000	8,9,11,13,15
Yellow-breasted Bowerbird	26.5-29 cm	71-97 cm	48-66 cm	>4000	50 - 1000	1,2,11
Fawn-breasted Bowerbird	28-30 cm	50-168 cm	51-81 cm	?	50 - >100	1,2,16

References: 1 = Gilliard 1969; 2 = Coates 1990; 3 = Bell 1970; 4 = Mackay 1989; 5 = this study; 6 = Marshall 1954; 7 = Vellenga 1970; 8 = Veselovský 1979; 9 = Borgia 1995a; 10 = Serventy 1955; 11 = Cooper & Forshaw 1977; 12 = Chaffer 1945; 13 = Warham 1962; 14 = Borgia & Mueller 1992; 15 = Veselovský 1978; 16 = Peckover 1970. * = northern taxon; ** = southern taxon (see Chapter 3).

Satin Bowerbirds. Regent Bowerbird males have been seen stealing objects from Satin Bowerbird bowers. However, access to this resource was probably limited due to the presence of the bower-owning Satin Bowerbird, a larger species. That Regent Bowerbird males do utilize man-made blue objects as bower decorations may support the suggestion that suitable natural blue objects are sought but are seldom found by the birds.

The two types of vegetable objects found regularly in Regent Bowerbird bowers in the Sarabah Range, green leaves and Deep Yellow-wood fruit, were definitely not in short supply. Deep Yellow-wood is a tree species of rainforest fringes (STANLEY & ROSS 1983) and has certainly increased in abundance due to logging activities in the study area (see Chapter 2). At least nowadays a large supply of Deep Yellow-wood fruit would be available, if they were of particular importance for the mating success of bower owners. The use and supply of vegetable objects found in Regent Bowerbird bowers in the Green Mountains is difficult to assess, as only few bowers could be studied, while an enormous diversity of plant species is found in this area (MCDONALD & WHITEMAN 1979; MCDONALD & THOMAS 1989).

Overall, none of the decoration types used by Regent Bowerbirds appears to be particularly rare in their present environment, although some objects (e.g. snail shells, cicada exuviae, pieces of blue plastic) may be less abundant than others. The same probably applies to Flame and Fire-maned Bowerbirds, which use small numbers of snail shells, leaves and fruits of various colours as bower decoration (GILLIARD 1969; BELL 1970; MACKAY 1989; COATES 1990). Therefore, it is likely that differences in the function of the bower in the mating system between the *Sericulus* species and other bowerbird genera are responsible for the much smaller bower dimensions and numbers of decoration objects of the *Sericulus* species.

BORGIA (1985a) found that several measures of bower quality (e.g. symmetry of structure, stick density) were correlated with the reproductive success of male Satin Bowerbirds. In contrast, the fact that Regent Bowerbirds used significantly thicker sticks than the larger Satin Bowerbirds suggests that the quality of the bower construction may be less important.

Several bowerbird species have been found to gather decoration objects with colours matching the plumage of conspecific adult males (MORRISON-SCOTT 1937; MARSHALL 1954; DONAGHEY et al. 1985; BORGIA & MUELLER 1992). In Regent Bowerbird bowers, objects with colours somewhat similar to the black and yellow plumage of conspecific adult males have been found only occasionally, such as black fruit (RAMSAY 1867; GODDARD 1947; VESELOVSKÝ 1979), red fruit (RAMSAY 1867; VESELOVSKÝ 1979), golden flowers (MARSHALL 1934) and orange fungi (WHEELER 1973). In Sarabah Range bowers, a piece of golden foil was the only decoration object with some similarity to the plumage of adult male Regent Bowerbirds. Other items with similar colours were available in the study area but not used, such as the yellowish to orange fruit of the Small-leaved Fig *Ficus obliqua*.

Blue decoration objects have been found in bowers of a number of species, including all *Sericulus* species (GILLIARD 1969; BELL 1970; DIAMOND 1982a, 1986b; MACKAY 1989; COATES 1990). DIAMOND (1982a, 1986b) suggested that blue fruits used by male Golden-fronted Bowerbirds during courtship display afford maximum colour contrast against the background of the males' golden-orange crest. The use of blue objects by *Sericulus* males could result in a similar colour contrast against the orange-yellow crown and nape of the males. While the blue objects found in bowers of Flame and Fire-maned Bowerbirds were fruit (GILLIARD 1969; BELL 1970; MACKAY 1989; COATES 1990), Regent Bowerbirds in the Sarabah Range and in the Green Mountains used pieces of blue plastic. Regent Bowerbirds regularly fed on blue drupes of the Blueberry Ash *Elaeocarpus obovatus* (see Chapter 4), but these drupes were unavailable during mating seasons as they ripen later.

PRUETT-JONES & PRUETT-JONES (1988) found that males of a court-clearing bird of paradise, Lawes' Parotia *Parotia lawesii*, collect objects at their courts which females may use as mineral supplement or as nest-lining material. Bowerbird males, however, generally decorate bowers with objects which are neither edible nor otherwise useful resources for females, and there is no evidence that females take any objects from bowers (BORGIA et al. 1985). This also applies to Regent Bowerbirds and their bowers, only few of which contained any edible objects.

MARSHALL (1954, p. 118) emphasized that the Regent Bowerbird's bower, "however small, is apparently an adequate vehicle for its sexual display, and such being the case, there is no reason for it to be any bigger or more lavishly decorated than it is". Observations of the interactions at bowers and data on the way bowers and decoration objects are used in courtship display and sexual competition are required to understand the function of the bower in the mating system of this species.

Site selection and spatial distribution of bowers

According to G. BORGIA (in BORGIA et al. 1985, p. 233), Regent Bowerbirds "are most active in dense rainforest, yet their bowers appear to be built in adjacent second-growth areas". No further details were given, and BORGIA did not explain what "are most active" means. Data on the bower site selection by Regent Bowerbirds (Tables 6.8-6.9), however, support BORGIA's view that males of this species frequently select regrowth sites for bower building, with a comparatively low and more open canopy.

BORGIA et al. (1985) also suggested that bowerbirds typically build display sites in more open habitats than court-clearing birds of paradise, such as the *Parotia* species and the Magnificent Bird of Paradise *Cicinnurus magnificus* (see COATES 1990). In this respect, the Regent Bowerbird differs from most other bowerbird species: bower sites analysed in the Sarabah Range were characterized by a comparatively small percentage of open forest floor and a large percentage of liana-thicket cover (Table 6.8).

The denseness of the thickets in which most bowers were found, often made it difficult to envisage how the birds should perform a display in the midst of the dense vegetation. Three explanations could account for this pattern of bower-site selection: (a) the dense thicket could provide protection from predators for the birds during bower maintenance and courtship displays; (b) the thicket could constitute an important component of a site because males sing and posture from certain lianas during their courtship display; (c) the thicket could make bowers more difficult for conspecific males to visually locate and/or easily approach.

For potential avian predators, such as Brown Goshawk *Accipiter fasciatus* and Grey Goshawk *A. novaehollandiae*, it is almost impossible to attack birds sitting under dense liana vegetation. On the other hand, potential reptilian predators, such as the Carpet Python *Morelia spilota*, can lie in the thicket in wait for prey. Therefore, it is possible that the dense vegetation of bower sites provides protection from some, but not all, potential predators. Considering the small size of Regent Bowerbird bowers, it is also possible that the surrounding lianas are used as perches during displays and that they conceal bowers from conspecific males.

The pronounced differences between Regent and Satin Bowerbirds in their bower-site selection (Tables 6.10-6.11) suggest that there is much less habitat overlap between males of the two species than expected by GILLIARD (1969). Satin Bowerbirds and their bowers are mainly found along rainforest fringes and in woodland (DONAGHEY 1981). Regent Bowerbird bowers in the Sarabah Range were found significantly farther away from the edge of the rainforest than the bowers of Satin Bowerbirds.

Could it be that Regent Bowerbirds, the smaller of the two species, avoid the edge of the rainforest due to interspecific competition with Satin Bowerbirds? It has been observed that Satin Bowerbirds attend and destroy Regent Bowerbird bowers which were close to the rainforest edge (BARDEN 1977; G. THRELFO pers. comm.). These incidents, however, appear to be rare. During the course of the field work for this study, Satin Bowerbirds never visited any Regent Bowerbird bower, although up to several dozen Satin Bowerbirds were observed in the study area and several of their bowers were found. The Regent Bowerbird population in the Clarke Range west of Mackay (see Table 3.4) is found in an area where Satin Bowerbirds are absent (see BLAKERS et al. 1984), but this population does not appear to frequent rainforest fringes more often than populations occurring sympatrically with Satin Bowerbirds (N.W. LONGMORE pers. comm.). Therefore, there is little evidence supporting the view that the bower-site selection of Regent Bowerbirds is strongly influenced by Satin Bowerbirds.

Regent and Satin Bowerbirds are not the only pair of bowerbird species with sympatric populations and similar display sites: though to a lesser extent, the ranges of Spotted Bowerbirds *Chlamydera maculata* and Great Bowerbirds *C. nuchalis*, of Great and Fawn-breasted Bowerbirds, and of Fawn-breasted and Yellow-breasted Bowerbirds *C. lauterbachi* also overlap in several areas (BLAKERS et al. 1984; COATES 1990). None of these species seems to replace another species through interspecific competition at bower sites, although birds have been observed to visit bowers of other species (GILLIARD 1969; FRITH et al. 1995). However, species building a similar type of bower (maypole bower or avenue bower, see Chapter 1) have much more often allopatric or parapatric ranges than sympatric ranges (MARSHALL 1954; GILLIARD 1969). It may be that Regent and Satin

Bowerbirds are the only species with largely overlapping ranges and a similar type of bower because their rainforest environment offers them a very diverse habitat.

The finding that Regent Bowerbird bowers have an avenue less close to a north-south orientation than avenues of Satin Bowerbird bowers may be related to the differences in their bower sites. MARSHALL (1954) suggested that Satin Bowerbirds orientate bowers across the path of the sun. This may be less important at the bower sites of Regent Bowerbirds, where most sunlight comes through a gap in the canopy just above the bower and only very little sunlight comes from the sides. Moreover, Regent Bowerbirds place their decoration objects within the avenue, in contrast to other avenue-building species which prefer one entrance of the avenue to spread their objects (SERVENTY 1955; PECKOVER 1970; VELLENGA 1970; VESELOVSKÝ 1978, 1979; BORGIA et al. 1985), or spread the decorations in nearly equal numbers at both ends of the bower (BORGIA 1995a).

The mean nearest-neighbour distance of 195 m between Regent Bowerbird bowers is similar to data for other bowerbird species found in forests: PRUETT-JONES & PRUETT-JONES (1982) found a mean nearest-neighbour distance of 169 m for Macgregor's Bowerbirds, DONAGHEY (1981) found 284 m for Satin Bowerbirds in rainforest and 311 m in woodland. Interbower distances are greater in species of more open habitats: PECKOVER (1970) found 560 m for Fawn-breasted Bowerbirds, BORGIA & MUELLER (1992) found slightly less than 2 km for Spotted Bowerbirds, and VESELOVSKÝ (1978, 1979) found more than 2 km for Great Bowerbirds.

The fact that most Regent Bowerbird bowers in the Sarabah Range were situated close to the ridgetop resembles the preference for sites along ridges found in several other bowerbird species (DIAMOND 1982a, 1987; PRUETT-JONES & PRUETT-JONES 1982; CROME & MOORE 1989; GRANT & LAURANCE 1990; FRITH & FRITH 1995). However, Regent Bowerbird bowers have also been found in completely flat lowland areas, such as the littoral rainforest in the Iluka Nature Reserve (CHAFFER 1984 and in litt.). It is possible that Regent Bowerbirds in the Sarabah Range simply preferred bower sites close to the ridgetop because these were flatter than sites on the slopes. Along the ridge, the Regent Bowerbird bowers were not clumped but were widely spaced. A similar dispersion of bower sites has been found in most other species (DONAGHEY 1981; PRUETT-JONES & PRUETT-JONES 1982; BORGIA 1986a; DIAMOND 1986b; CROME & MOORE 1989). Only the Tooth-billed Bowerbird is now regarded as forming exploded leks with aggregated display sites at mean nearest neighbour distances of little more than 50 m (G. BORGIA pers. comm.; FRITH & FRITH 1995).

An understanding of the dispersion of Regent Bowerbird bowers is complicated by the large number of rudimentary bowers (Table 6.2). An unknown number of the rudimentary bowers have been remnants of destroyed, formerly active bowers; this made it impossible to apply more advanced methods to analyse the pattern of bower dispersion. CHAFFER (1984 and in litt.) observed a similarly large proportion of rudimentary bowers of Regent Bowerbirds in the Iluka Nature Reserve. Observations on the patterns of bower maintenance and male interactions are required to understand why more than half of the Regent Bowerbird bowers were found in a rudimentary state.

7 Mating Behaviour and Sexual Competition

7.1 Introduction

In polygamous species there are various ways in which individuals may acquire, and compete for, mates (EMLEN & ORING 1977; ORING 1982; DAVIES 1991): individuals may defend resources to which members of the opposite sex are attracted, they may directly defend the members of the opposite sex, or they may put all their efforts into advertising themselves with visual and/or acoustic displays. Among the best-known examples of the latter are the spectacular sexual displays of some bird species, such as species of grouse (JOHNSGARD 1983), the Ruff *Philomachus pugnax* (HOGAN-WARBURG 1966, 1992), cotingas (SNOW 1982), manakins (SNOW 1962a,b; LILL 1974a, 1976), lyrebirds (SMITH 1988; ROBINSON & CURTIS 1996) and birds of paradise (GILLIARD 1969; COOPER & FORSHAW 1977; BEEHLER & PRUETT-JONES 1983; COATES 1990; FRITH & BEEHLER 1998).

Males of the non-monogamous bowerbird species perform their sexual displays, and mate, at their courts or bowers (GILLIARD 1959, 1969; WARHAM 1962; COOPER & FORSHAW 1977; VESELOVSKÝ 1978, 1979; PRUETT-JONES & PRUETT-JONES 1983, 1994; BORGIA et al. 1985; FRITH & FRITH 1989, 1998a; COATES 1990). It has been shown that bower quality and the number of decoration objects influence female mate-choice decisions (BORGIA 1985a, 1986a, 1995b; BORGIA & MUELLER 1992).

In several bowerbird species it was observed that males destroy bowers of other males and/or steal decoration objects from them (VELLENGA 1970, 1980b, 1986; PRUETT-JONES & PRUETT-JONES 1982, 1983, 1994; BORGIA 1985b, 1995a,b; BORGIA & GORE 1986; DIAMOND 1986a, 1987, 1988; FRITH 1989; FRITH & FRITH 1989, 1994b, 1998a; BORGIA & MUELLER 1992). As bowers and decorations are key elements of the sexual display of bowerbirds, bower destruction and decoration stealing represent patterns of sexual competition through which males affect the mating success of their competitors and themselves (BORGIA 1985b; BORGIA & GORE 1986; BORGIA & MUELLER 1992; PRUETT-JONES & PRUETT-JONES 1994).

The mating behaviour of the Regent Bowerbird and the patterns of sexual competition in this species are poorly known. Few people have seen the sexual display of adult males. With the exception of some brief and vague notes (CAMPBELL 1900; MARSHALL 1954; BARDEN 1977; COOPER & FORSHAW 1977), mainly based on observations of subadult males, the sexual display of the Regent Bowerbird has not been described in the literature. Prior to this study, copulation has been recorded only once (THRELFO 1985). Factors influencing female mate choice, and the occurrence of bower destruction and decoration stealing in Regent Bowerbirds are unknown.

BELL (1970) suggested that Regent Bowerbirds and the congeneric *Sericulus* species in New Guinea may maintain their bowers for a very short time only. This would be a striking difference to other genera, in which bower-owning males show a strong fidelity to their bower site, often maintain the same bower over several consecutive mating seasons, or build a new bower only a few metres from a site used previously (GILLIARD & LECROY 1966; PECKOVER 1970; HOPKINS 1974; VELLENGA 1980b; DONAGHEY 1981; DIAMOND 1987; CROME & MOORE 1989; FRITH 1989; COATES 1990; FRITH & FRITH 1998a).

If BELL's suggestion that *Sericulus* males use bowers for a short time only is correct, a time budget approach may assist in discerning this. Time budgets show how animals allocate their available time to different activities. According to optimality models, selection tends to produce outcomes "that represent the best achievable balance of costs and benefits" (KREBS & KACELNIK 1991, pp. 105-106). This approach has frequently been used in studies on foraging behaviour (KREBS 1978; BEGON et al. 1986; FORD 1989), but may also be used when studying mate-searching behaviour (PARKER 1978; SUTHERLAND 1987). For example, knowing the time male Regent Bowerbirds devote to bower-maintenance activities could help in understanding the constraints upon continuing to maintain an old bower or building a new one. Thus, knowledge of the patterns of bower maintenance could also help in explaining the small size of Regent Bowerbird bowers, the small number of decoration objects and the frequency of rudimentary bowers in this species (see Chapter 6).

This chapter shall describe the behaviour of Regent Bowerbirds at their bowers. Time budgets of bower-owning males, the sexual display, patterns of female visits and male interactions at bowers shall be analysed, in order to provide a basis for a comparison of the mating behaviour and sexual competition in the Regent Bowerbird with other bowerbird species.

7.2 Methods

Each of the 33 active Regent Bowerbird bowers found in the Sarabah Range during the three mating seasons studied (see Table 6.2) was monitored as long as the bower was maintained and visited by birds. Bower activities were observed from hides (see Chapter 2), which were erected 8-12 m away from bowers, depending on topography and vegetation of the site.

A total of 1516 hours on 211 days was spent monitoring bower activities; the time spent at each bower is given in Table 7.1. A total of 1461 hours was spent at 29 bowers of adult males, and 55 hours were spent at 4 bowers of subadult males. The observation time differed between bowers due to the differences in the number of days bowers were maintained. Most bowers were monitored daily until they had been destroyed and/or had been abandoned by the birds. Hide observations were conducted between 5.00 and 18.15 h Eastern Standard Time. During the third field season, most hide sessions were terminated earlier in the day, after the data gathered in the two previous field seasons had shown reduced bower attendance in the late afternoon hours.

Table 7.1. History of 33 active bowers of Regent Bowerbirds. H = number of hours bower was monitored; D = number of days bower was monitored; Ad. = adult; Sub. = subadult; unb. = unbanded individual; ? = bower was destroyed but the act of destruction was not observed; - = bower was not destroyed but disintegrated naturally after the mating season.

Tab. 7.1. Werdegang von 33 als Balzplatz genutzten und unterhaltenen Gelbnacken-Laubenvogel-Lauben. H = Anzahl der Stunden der Laubenüberwachung; D = Anzahl der Tage der Laubenüberwachung; Ad. = adult; Sub. = subadult; unb. = unberingtes Individuum; ? = Laube wurde zerstört, doch der Hergang der Laubenzerstörung wurde nicht beobachtet; - = Laube wurde nicht zerstört, sondern zerfiel nach der Paarungssaison.

Bower No.	Date when bower was found	Date when bower was destroyed	Owner of bower	Destroyer of bower	H	D
Mating season 1989:						
1.	8 Oct. 1989	14 Oct. 1989	Ad. unb.	?	26	3
2.	11 Oct. 1989	15 Oct. 1989	Ad. RRR	?	6	2
3.	8 Nov. 1989	8 Nov. 1989	Ad. unb.	Ad. unb.	3	1
4.	12 Nov. 1989	-	Ad. unb.	-	208	23
5.	17 Nov. 1989	26 Nov. 1989	Ad. unb.	?	9	5
Mating season 1990:						
10.	23 Sep. 1990	27 Sep. 1990	Ad. RRR	Sub. GRN	51	6
15.	30 Sep. 1990	5 Oct. 1990	Ad. unb.	?	36	5
20.	8 Oct. 1990	9 Oct. 1990	Sub. NBR	Ad. unb.	12	2
31.	22 Oct. 1990	2 Nov. 1990	Ad. RGR	Sub. NBR	111	12
32.	25 Oct. 1990	27 Oct. 1990	Ad. RBN	Sub. NRB	24	3
35.	1 Nov. 1990	8 Nov. 1990	Ad. unb.	Ad. RNR	52	8
38.	5 Nov. 1990	10 Nov. 1990	Ad. unb.	Ad. unb.	38	5
42.	14 Nov. 1990	17 Nov. 1990	Ad. RWN	Ad. NNB	35	4
46.	17 Nov. 1990	19 Nov. 1990	Ad. RGR	Ad. unb.	16	2
50.	27 Nov. 1990	-	Ad. RBN	-	166	19
52.	4 Dec. 1990	6 Dec. 1990	Ad. RWN	Ad. RWW	34	4
54.	11 Dec. 1990	-	Ad. RWW	-	68	9
55.	13 Dec. 1990	15 Dec. 1990	Ad. RWW	Ad. RNR	18	4
56.	26 Dec. 1990	31 Dec. 1990	Sub. RGG	?	28	5
57.	4 Jan. 1991	-	Sub. NBN	-	13	3
58.	16 Feb. 1991	-	Sub. RGG	-	2	1
Mating season 1991:						
59.	28 Sep. 1991	1 Oct. 1991	Ad. RBN	Ad. RRR	27	4
61.	6 Oct. 1991	20 Oct. 1991	Ad. unb.	Ad. RNR	86	10
62.	8 Oct. 1991	9 Oct. 1991	Ad. RRR	Ad. RBN	15	2
64.	12 Oct. 1991	14 Oct. 1991	Ad. RWN	Ad. RWW	21	3
65.	15 Oct. 1991	15 Oct. 1991	Ad. RWN	Ad. RWW	8	1
66.	18 Oct. 1991	28 Oct. 1991	Ad. GWW	Ad. RRR	87	10
67.	23 Oct. 1991	11 Nov. 1991	Ad. RWN	Ad. RRR	126	17
68.	28 Oct. 1991	18 Nov. 1991	Ad. RBN	?	51	10
70.	9 Nov. 1991	14 Dec. 1991	Ad. NNB	Ad. RWN	63	11
71.	4 Dec. 1991	21 Dec. 1991	Ad. RNR	?	51	11
72.	8 Dec. 1991	10 Dec. 1991	Ad. RWN	Ad. RWN	15	3
74.	11 Jan. 1992	13 Jan. 1992	Ad. NRB	?	10	3
33 active bowers					1516	211

True continuous recording (see MARTIN & BATESON 1986) was employed to quantify bower activities during all daylight hours, recording time of onset and termination of behaviour patterns in seconds. This recording method obtains measures for both events and states of behaviour patterns, i.e. frequencies and durations (ALTMANN 1974; MARTIN & BATESON 1986). This made it possible to calculate time budgets of bower-owning males (following DONAGHEY 1981; PRUETT-JONES & PRUETT-JONES 1982; LILL 1986), i.e. the average percentage of daylight hours males spent in some activity (behavioural state), as well as the number of occurrences (events) of, for example, visits by females or intruding males.

Bower maintenance and display activities were video-recorded, using a Sony Video 8 camera recorder Handycam 2006i EVC-X10, a Sony electret condenser microphone ECM-Z200 with zoom control (directivity changeable from uni-directional to super cardioid characteristics), and a Fujinon TV zoom lens H6X12.5R 1:1.2/12.5-75 mm. This system made it possible to film the birds during all daylight hours, even very early in the morning, without using artificial light, and to tape their rather soft vocalizations. Display postures were drawn from videotapes using still pictures and frame-by-frame playback.

Elements of behaviour, in particular the structure of sexual displays (courtship displays), were described using neutral terms (MARTIN & BATESON 1986), unless the effects of the behaviour were as unambiguous as, for example, in bower destruction. Wherever possible or appropriate, the terminology of previous studies on bowerbird behaviour (WARHAM 1957, 1962; GILLIARD 1959, 1969; VESELOVSKÝ 1979; DONAGHEY 1981; PRUETT-JONES & PRUETT-JONES 1982; BORGIA 1985a,b; FRITH & FRITH 1989; BORGIA & MUELLER 1992) was used to describe categories of behaviour.

To assess the quality of bowers and their decorations, the following measures were used: (a) the overall quality of the bower construction was evaluated using a subjective scale from '1' to '5', with bowers consisting of a large number of fine, straight, densely-packed sticks receiving the highest overall-quality rank, and bowers consisting of a small number of loosely-inserted sticks of different diameters receiving the lowest rank (following BORGIA 1985a,b); (b) the symmetry of the bower walls was assessed by dividing the height of the lower wall by the height of the higher wall, dividing the width of the narrower wall by the width of the wider wall, and adding up the two quotients (the sum of the two quotients is '2' for bowers with walls of identical height and width, and is smaller for bowers with less symmetrical walls); (c) all types of bower decoration were counted daily (see Chapter 6).

As the number of observed copulations was too small to use as a measure of male mating success, the duration of female visits was used as an indicator of female preferences. Durations of female visits have also been used as a variable in several other studies on mate choice in polygamous bird species (e.g. PRUETT-JONES & PRUETT-JONES 1990; ANDERSSON 1991). Spearman's rank correlation coefficients (SPATZ & JOHNSTON 1989), r_s, were used for statistical comparisons of bower measures and the duration of female visits.

In the third field season, three radio tags were obtained to radio-track bower-owning adult males. Unfortunately, one of the transmitters failed and could not be repaired in time, and one radio-tagged male lost his tag shortly after the tag had been attached; thus, only one male could be radio-tracked. The tag was glued to the male's lower back (following KENWARD 1987). It was tracked using a Titley Electronics Regal 2000 Telemetry Receiver and a three-element Yagi antenna. However, frequent movements of the bird, reflections of the radio waves by the dense vegetation, and limited time due to the time-consuming bower searches and observations resulted in only a small number of reliably-triangulated radio fixes. A minimum-area polygon was drawn to assess the home range area of the radio-tagged male (KENWARD 1987).

To assess the relative dominance of individual birds and of sex and age classes, agonistic interactions at an artificial feeding site in the centre of the study area (the baited trap, see Chapter 2) were observed (following BORGIA 1985b). For each aggressive encounter observed, the identities of attacker and victims as well as the outcome (i.e. the identity of the retreating individual) were recorded.

7.3 Results

7.3.1 Mating behaviour

Bower-owning males and their time budgets

The 33 active bowers which were monitored during this study were generally maintained by a single male, the bower owner (see Table 7.1). There were only two exceptions to this general pattern: subadult males often showed maintenance behaviour when visiting a bower of another male, and two adult males showed some maintenance behaviour at bowers that had been built, and were usually maintained, by other individuals (see section 7.3.2).

Several males maintained more than one bower within a mating season, with a maximum of four bowers in one mating season. In all except one of these cases, individual males did not maintain more than one bower simultaneously but maintained a new bower after the previous one had been destroyed. The only exception was observed in December 1990, when adult male RWW maintained bower 55 for three days while simultaneously maintaining bower 54 (see Table 7.1). The two bowers of RWW were 117.5 m apart (see Figs 6.2 and 7.9).

The total number of bowers owned by a particular adult male was highly significantly correlated with the number of days on which that individual was observed in the study area (Spearman's rank correlation, $r_s = 0.792$, $n = 29$, $P < 0.0001$). Eleven colour-banded adult males were observed on more than 50 days during this study and of these nine (81.8 %) were found to own at least one bower. Therefore, most of the adult males which were never found to own a bower visited the study area only rarely and may have maintained a bower outside the study area.

All distinguishable forms of behaviour of bower-owning males, within a 20 m radius of their bowers, are listed in Table 7.2 and are assigned to nine categories. The total time spent performing any of these categories of behaviour represents the entire bower attendance time of the owner.

Table 7.2. Categories of behaviour of bower-owning male Regent Bowerbirds at their bowers (within a radius of 20 m), chosen to calculate time budgets.
Tab. 7.2. Verhaltenskategorien von Lauben besitzenden Gelbnacken-Laubenvogel-Männchen an ihren Lauben (innerhalb eines Radius' von 20 m), die zur Berechnung von Zeitbudgets ausgewählt wurden.

Category	Behaviour of bower owner
Bower building	• pulls at a stick in vicinity of bower • breaks off a stick from shrub or tree • picks up a stick from forest floor • drops a rejected stick • inserts a stick into bower
Bower maintenance	• picks at and/or fixes a bower stick • masticates a leaf in bower avenue • paints inner avenue walls • rearranges decoration objects • removes a leaf from bower or vicinity • picks off a leaf from shrub or tree • puts a fresh leaf in avenue • pulls at a liana or root near bower • hops around bower looking at it • rebuilds damaged bower
Quietly perching	• looks around while quietly perched • preens while quietly perched • wipes bill while quietly perched
Vocalizing	• vocalizes while perched near bower
Courtship display	• displays to female at bower
Display to male	• displays to immature or subadult male
Solitary display	• displays solitarily at bower • sings solitarily at bower
Other interactions	• looks at an intruding male • flicks wings at an intruding male • chases intruding male conspecific or other bird
Bower destruction	• pulls sticks out of own bower • leaves bower with decoration in bill
Bower attendance	• total time spent performing any of these behaviours

The time investment of bower-owning adult males in categories of behaviour is summarized in Table 7.3. Adult males spent an average of 3.2 % of daylight hours attending their bowers (range 0.4-13.9 %). Most of the bower-attendance time was spent performing bower-building behaviour (22.9 % of attendance time) and bower-maintenance behaviour (38.6 % of attendance time). Less than 1 % of daylight hours was spent in activities involving vocalizations (i.e. vocalizing, courtship display, display to male, solitary display).

Table 7.3. Time investment of bower-owning adult male Regent Bowerbirds in categories of behaviour defined in Table 7.2, expressed as percentage of daylight hours and as percentage of bower-attendance time. Based on a total observation time of 1461 hours at 29 bowers.
Tab. 7.3. Zeitinvestition von Lauben besitzenden adulten Gelbnacken-Laubenvogel-Männchen in die in Tab. 7.2 definierten Verhaltenskategorien, ausgedrückt als prozentualer Anteil an den Tageslicht-Stunden und als prozentualer Anteil an der Anwesenheitszeit an der Laube. Basierend auf einer Gesamtbeobachtungszeit von 1461 Stunden an 29 Lauben.

Category of behaviour	% of daylight hours	% of bower-attendance time
Bower building	0.741 %	22.93 %
Bower maintenance	1.247 %	38.56 %
Quietly perching	0.552 %	17.08 %
Vocalizing	0.015 %	0.46 %
Courtship display	0.453 %	14.01 %
Display to male	0.079 %	2.43 %
Solitary display	0.107 %	3.30 %
Other interactions	0.008 %	0.24 %
Bower destruction	0.032 %	0.99 %
Bower attendance	3.234 %	100.00 %

The small percentage of daylight hours bower-owning adult males spent at or near their bowers was confirmed by the tracking of the radio-tagged individual. Of 24 triangulated fixes, only one (4.2 %) was within 50 m of the male's bower, seven (29.1 %) were 50-100 m away from the bower, six (25.0 %) were 100-200 m from the bower, six (25.0 %) were 200-300 m from the bower, three (12.5 %) were 300-400 m from the bower, and one fix (4.2 %) was more than 400 m away from the bower. A minimum-area polygon of the 24 fixes covered an area of 12.4 ha, and encompassed bower sites of at least four other adult males.

Bower-owning adult males visited their bowers at a mean rate of 0.43 ± 0.35 visits per hour (range 0.03-1.10 visits per hour). The mean duration of visits was 6.7 ± 4.4 minutes, ranging from five seconds, when the male flew away immediately after having a brief look at the bower, up to 42.4 minutes, when the male performed extensive bower-building and bower-maintenance activities. At the end of a bower visit, bower-owning adult males generally departed from their bowers by flying away rapidly (in 374 or 89.5 % of 418 observed visits); only rarely did they depart by slowly hopping upwards through the vegetation (in 44 or 10.5 % of 418 observed visits).

Bower-owning adult males attended their bowers during all daylight hours. The percentage of time they spent at their bowers at different times of the day is shown in Fig. 7.1. Most categories of behaviour were performed at all daylight hours. The category 'bower maintenance' was split up into 'painting' and 'other maintenance' in Fig. 7.1, and it is discernible that most painting was observed in the early hours of the morning (see Plate 31). Building was observed most often between 9.00 and 17.00 h, but only rarely between 5.00 and 9.00 h. Courtship display was observed between 5.00 and 17.00 h, but most often between 7.00 and 15.00 h.

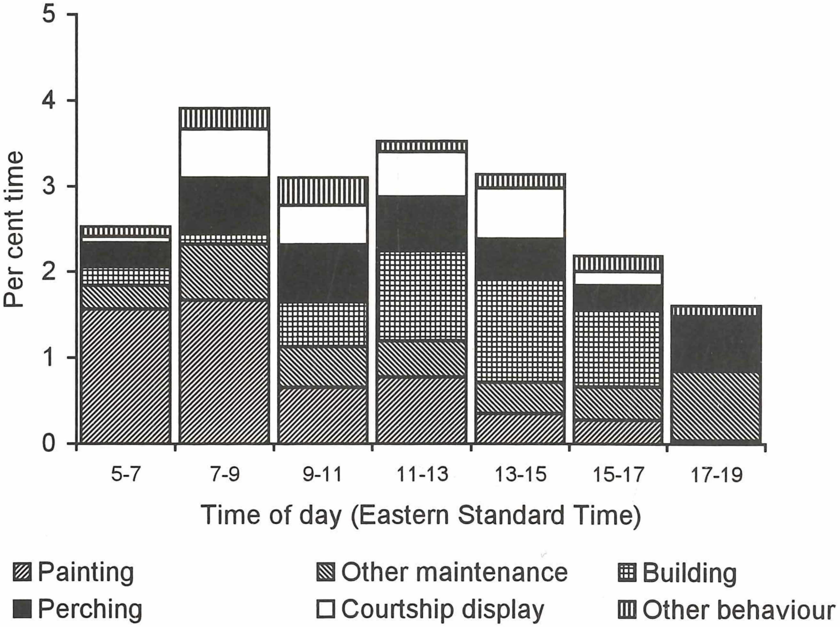

Figure 7.1. Percentage of time bower-owning adult male Regent Bowerbirds spent at their bowers at different times of the day (Eastern Standard Time) performing categories of behaviour defined in Table 7.2 (bower maintenance was split up into painting and other maintenance). Based on a total observation time of 1461 hours at 29 bowers.

Abb. 7.1. Prozentualer Zeitanteil, den Lauben besitzende adulte männliche Gelbnacken-Laubenvögel an ihren Lauben zu verschiedenen Tageszeiten (Ostaustralische Normalzeit) bei der Ausführung der in Tab. 7.2 definierten Verhaltenskategorien verbrachten ('bower maintenance' bzw. 'Laubeninstandhaltung' wurde in 'painting' bzw. 'Bemalen' und 'other maintenance' bzw. 'andere Instandhaltungsaktivitäten' aufgeteilt). Basierend auf einer Gesamtbeobachtungszeit von 1461 Stunden an 29 Lauben.

The time investment in the categories of behaviour defined in Table 7.2 by bower-owning subadult males is summarized in Table 7.4. Subadult males spent an average of 11.8 % of daylight hours attending their bowers (range 2.4-18.7 %), almost four times as much as adult males. This difference in bower-attendance time between subadult and adult males was highly significant (based on the number of minutes subadult and adult males spent attending their bowers and the number of minutes bowers were monitored but not attended, $\chi^2 = 684.2$, *d.f.* = 1, $P < 0.00001$). Subadult males spent more than half of their bower-attendance time performing solitary display (50.7 % of attendance time), compared to only 3.3 % solitary display during bower attendance of adult males (Table 7.3). This difference in time investment in solitary display between subadult and adult males was highly significant (based on numbers of minutes, $\chi^2 = 3444.8$, *d.f.* = 1, $P < 0.00001$). Subadult males also invested highly significantly more time in bower-building behaviour than adult males (based on numbers of minutes, $\chi^2 = 181.1$, *d.f.* = 1, $P < 0.00001$).

Table 7.4. Time investment of bower-owning subadult male Regent Bowerbirds in categories of behaviour defined in Table 7.2, expressed as percentage of daylight hours and as percentage of bower-attendance time. Based on a total observation time of 55 hours at 4 bowers.
Tab. 7.4. Zeitinvestition von Lauben besitzenden subadulten Gelbnacken-Laubenvogel-Männchen in die in Tab. 7.2 definierten Verhaltenskategorien, ausgedrückt als prozentualer Anteil an den Tageslicht-Stunden und als prozentualer Anteil an der Anwesenheitszeit an der Laube. Basierend auf einer Gesamtbeobachtungszeit von 55 Stunden an 4 Lauben.

Category of behaviour	% of daylight hours	% of bower-attendance time
Bower building	2.901 %	24.50 %
Bower maintenance	1.016 %	8.58 %
Quietly perching	1.228 %	10.37 %
Vocalizing	0.237 %	2.00 %
Courtship display	0.280 %	2.36 %
Display to male	0.115 %	0.97 %
Solitary display	6.000 %	50.67 %
Other interactions	0.066 %	0.55 %
Bower destruction	0.000 %	0.00 %
Bower attendance	11.843 %	100.00 %

Sexual display

Male Regent Bowerbirds perform sexual displays (courtship displays) at bowers (bower displays) and in trees (arboreal displays). Arboreal displays are less intense and contain only a part of the elements of bower displays. Therefore, bower displays are described first.

Initial bower display: The male stands at an entrance of the bower avenue in an upright posture and starts to utter his display song, a low, soft chattering and warbling, while looking upward to the female that is perching on a branch a few metres above the bower. Once the female arrives at the bower, the male moves back c. 20 to 50 cm. The male either stands in front of the bower or perches on a nearby branch or liana and continues to sing, facing the female, while the female sits in the bower avenue or in an entrance of it and looks around. During this initial part of the display, some females briefly peck at the decoration objects in the avenue.

If the female continues to stay, the male starts the main bower display. Following descriptions of the displays of Spotted and Great Bowerbirds by WARHAM (1962), the main bower display of the Regent Bowerbird can be divided into 'central display' and 'peripheral display'. The two terms mainly refer to the place where the display is performed, and do not represent a fixed sequence of postures, though central display is performed more often in an early stage of the bower display, and peripheral display more often in a later stage.

Central bower display: During central bower display, the male stays close to the bower, not more than c. 30 cm away from one of the two entrances of the avenue. During most of the central display, the male stands in an upright posture in an entrance of the avenue, facing the female. Occasionally, the male picks up a decoration object from the avenue and holds it in his bill (see Fig. 7.2), while making sideways head movements. In the same upright posture, after dropping the decoration object back into the avenue, the male may gape, while moving the head to one side. In a slightly lowered posture, the male performs wing flicks, quickly opening and folding one wing (see Fig. 7.3). In a similar, slightly lowered posture, nape presentations are performed (see Fig. 7.4): the male looks away from the female, thus having the nape facing the female (Fig. 7.4a); the male then moves the head down, thus slightly lifting the nape (Fig. 7.4b); finally, the male moves the head back, whilst making a series of bobbing movements (Fig. 7.4c). During nape presentations the velvety yellow nape feathers may be raised c. 5 mm.

In a bent-forward posture, the male raises and repeatedly flaps both wings, while the bill is opened. During forehead presentations, the head is bent downward and the wings are slightly drooped; in this posture, the male darts forwards in a running (not hopping!) manner of locomotion, with the reddish forehead facing the female (see Fig. 7.5). This forehead-presentation advance towards the female may be repeated several times, the male returning to his pre-advance position by running backwards.

In the postures performed during central bower display, the yellow irides may suddenly become more conspicuous, because the pupils are contracted. The postures may be performed in various sequences; for example, a forehead-presentation advance may lead to a nape presentation, or to an upright posture with decoration object in bill (when an object was picked up from the avenue at the end of the advance).

Peripheral bower display: During peripheral bower display, the male darts around in the surroundings of the bower (see Fig. 7.6), within a radius of one metre.

Figure 7.2. Adult male Regent Bowerbird in an upright posture with decoration object (snail shell) in bill, while standing in entrance of bower avenue during central bower display, facing the female (drawn after videotape).
Abb. 7.2. Adulter männlicher Gelbnacken-Laubenvogel in Aufrechtpose mit Dekorationsobjekt (Schneckengehäuse) im Schnabel, während der zentralen Laubenbalz im Eingang der Laubenallee dem Weibchen gegenüberstehend (nach einem Videoband gezeichnet).

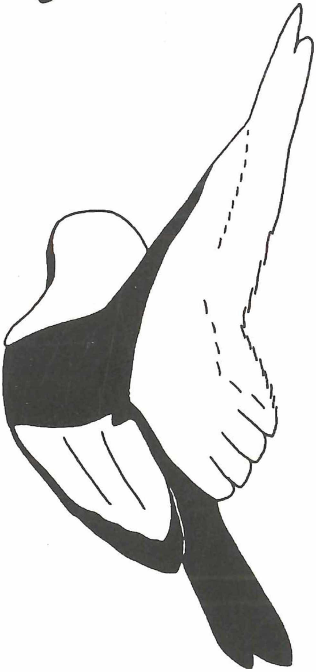

Figure 7.3. Adult male Regent Bowerbird performing a wing flick while standing in entrance of bower avenue during central bower display, facing the female (drawn after videotape).
Abb. 7.3. Adulter männlicher Gelbnacken-Laubenvogel bei einem schnellen Flügelschlag, während der zentralen Laubenbalz im Eingang der Laubenallee dem Weibchen gegenüberstehend (nach einem Videoband gezeichnet).

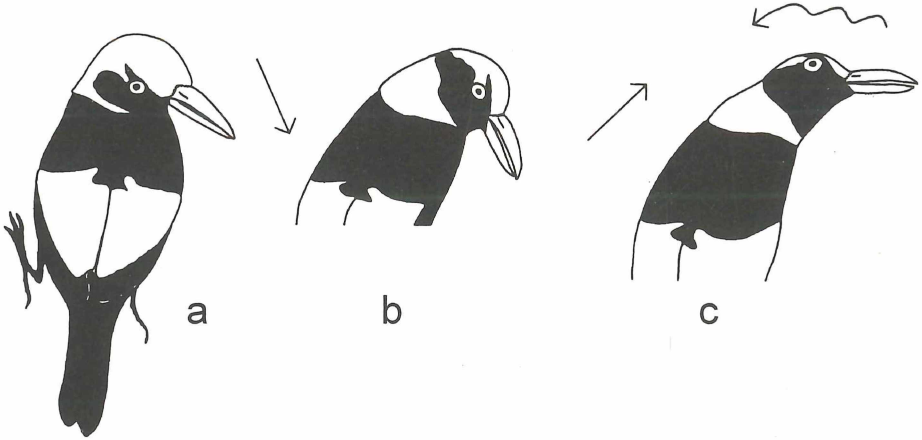

Figure 7.4. Adult male Regent Bowerbird performing a nape presentation while standing in entrance of bower avenue during central bower display: (a) looking away from the female, thus having the yellow nape facing the female; (b) moving the head down, thus slightly lifting the nape; (c) moving the head back, whilst making a series of bobbing movements (drawn after videotape).
Abb. 7.4. Adulter männlicher Gelbnacken-Laubenvogel bei einer Nackenpräsentation, während der zentralen Laubenbalz im Eingang der Laubenallee stehend: (a) vom Weibchen wegsehend, dadurch den gelben Nacken dem Weibchen zuwendend; (b) den Kopf herunterbewegend, dadurch den Nacken etwas anhebend; (c) den Kopf zurückbewegend, dabei eine Reihe von Aufundabbewegungen machend (nach einem Videoband gezeichnet).

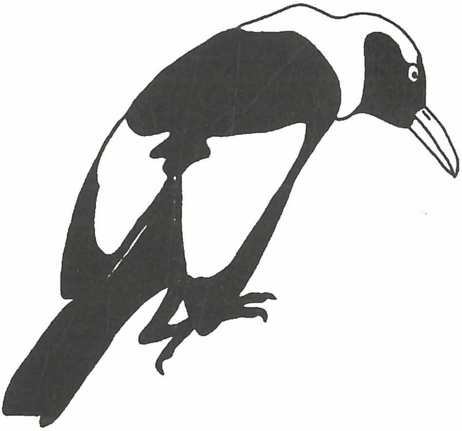

Figure 7.5. Adult male Regent Bowerbird performing a forehead presentation with the head bent downward during central bower display, the reddish forehead facing the female, and the wings slightly drooped (drawn after videotape).
Abb. 7.5. Adulter männlicher Gelbnacken-Laubenvogel bei einer Stirnpräsentation mit heruntergeneigtem Kopf, während der zentralen Laubenbalz, die rötliche Stirn dem Weibchen zuwendend, die Flügel etwas herabhängen lassend (nach einem Videoband gezeichnet).

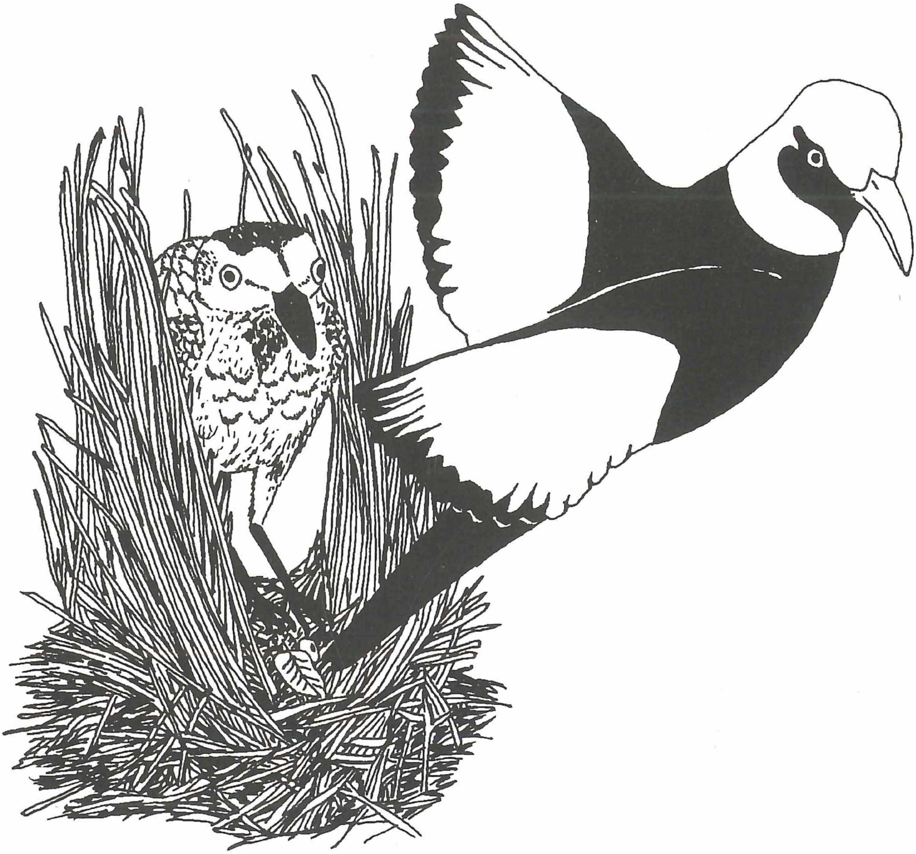

Figure 7.6. Adult male Regent Bowerbird flying in front of bower during peripheral bower display, while the female sits in the bower avenue, watching the male (drawn after videotape). All figures depicting elements of the bower display (Figs 7.2-7.8) were drawn in this perspective, viewed from the hide, with the displaying male in between hide and bower.
Abb. 7.6. Adulter männlicher Gelbnacken-Laubenvogel während der peripheren Laubenbalz vor der Laube fliegend, während das Weibchen in der Laubenallee sitzt, das Männchen beobachtend (nach einem Videoband gezeichnet). Alle Abbildungen, die Elemente der Laubenbalz darstellen (Abb. 7.2-7.8), wurden in dieser Perspektive gezeichnet, vom Tarnzelt aus betrachtet, mit dem balzenden Männchen zwischen Tarnzelt und Laube.

The generally abrupt movements of the male during peripheral bower display include flying, hopping and running around the bower and amongst nearby branches or lianas. When a wing is fully opened during flight, it creates a flash of bright yellow (see Fig. 7.7). When briefly perching near the bower, the male performs wing presentations, repeatedly opening and folding one wing (see Fig. 7.8). While the male performs most postures facing the female during central bower display, the male is often behind the female during peripheral bower display. The female, however, does not move and remains sitting or crouching in the bower.

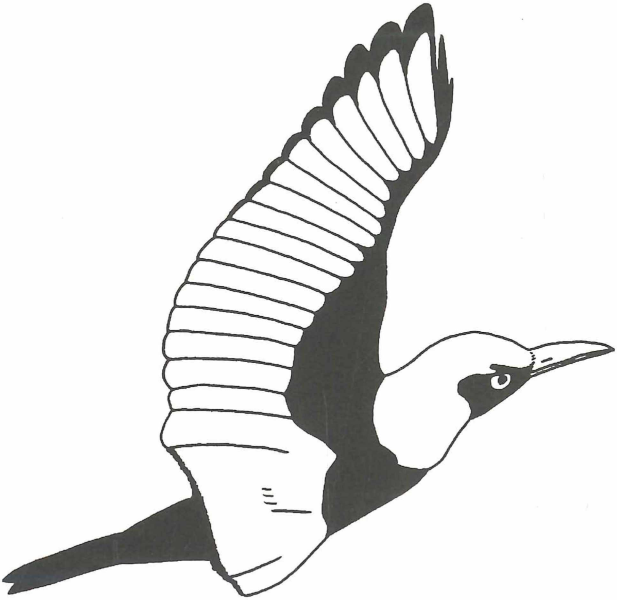

Figure 7.7. Adult male Regent Bowerbird flying near bower during peripheral bower display with the right wing, which is facing the female, fully opened (drawn after videotape).
Abb. 7.7. Adulter männlicher Gelbnacken-Laubenvogel während der peripheren Laubenbalz nahe der Laube fliegend, den rechten Flügel, der dem Weibchen zugewandt ist, ganz geöffnet (nach einem Videoband gezeichnet).

Vocalizations during bower display: The male sings continuously throughout bower display, even while holding a decoration object in his bill. The song includes mimicry of vocalizations of other bird species (e.g. Spectacled Monarch *Monarcha trivirgatus* and White-browed Scrubwren *Sericornis frontalis*), but vocal mimicry is often difficult to identify due to the low volume. The male may briefly stop singing when advancing towards the female in forehead-presentation posture during central bower display, or when flying amongst branches or lianas during peripheral bower display. When the female backs out of the avenue and hops to a nearby branch or liana, the song becomes slightly louder, though still considerably softer than the display vocalizations of males of other bowerbird genera.

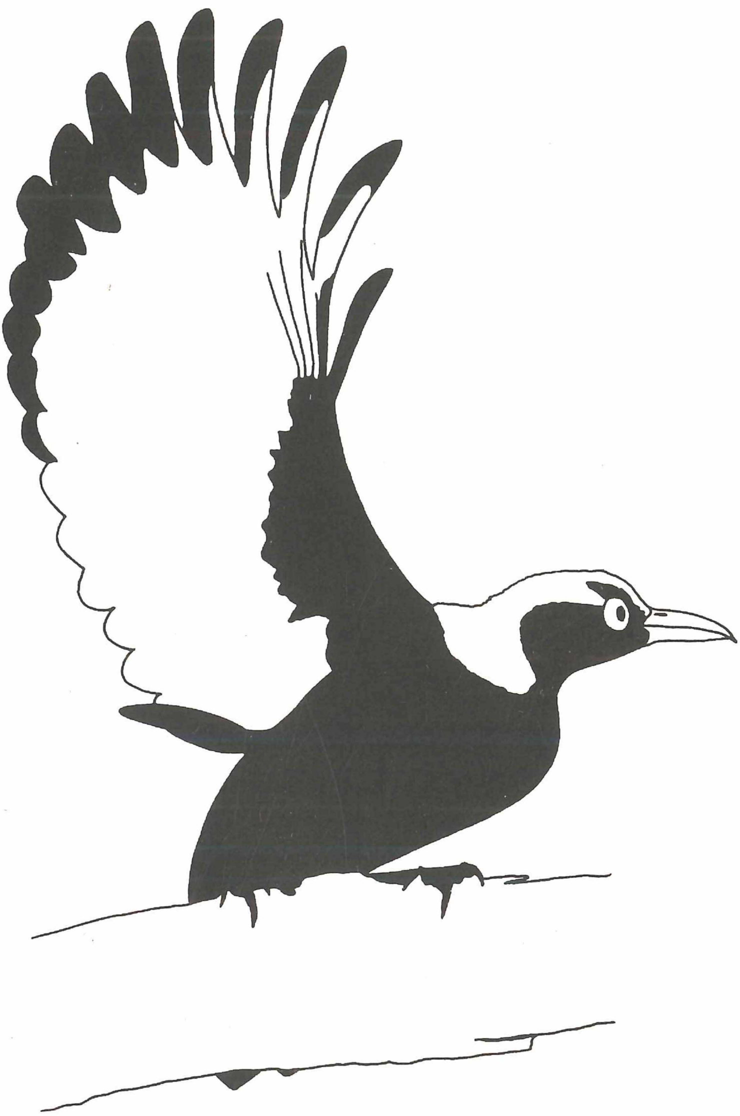

Figure 7.8. Adult male Regent Bowerbird performing a wing presentation while perching near bower during peripheral bower display (drawn after a photograph by NORMAN CHAFFER in CHAFFER 1984).
Abb. 7.8. Adulter männlicher Gelbnacken-Laubenvogel bei einer Flügelpräsentation, während der peripheren Laubenbalz nahe der Laube sitzend (gezeichnet nach einer Fotografie von NORMAN CHAFFER in CHAFFER 1984).

Use of decoration objects during bower display: The use of decoration objects in courtship displays at bowers is summarized in Table 7.5, which compares the number of times a certain type of bower decoration was picked up by a male from the avenue of his bower and held in his bill (see Fig. 7.2), while facing the female, with the number of times this type of decoration object was present but not used. Certain types of decoration objects were not used at a frequency corresponding to the frequency of their presence in bowers (9x2 contingency analysis, $\chi^2 = 27.57$, $d.f. = 8$, $P < 0.001$). Pieces of blue plastic were used less often than expected from the frequency of their presence in bowers ($\chi^2 = 6.10$, $d.f. = 1$, $P < 0.02$), while Deep Yellow-wood fruit was used more often ($\chi^2 = 13.31$, $d.f. = 1$, $P < 0.0005$).

Table 7.5. Use of decoration objects by male Regent Bowerbirds during courtship displays at their bowers ($n = 53$ decoration objects used).
Tab. 7.5. Verwendung von Dekorationsobjekten während der Arenabalz von männlichen Gelbnacken-Laubenvögeln an ihren Lauben ($n = 53$ verwendete Dekorationsobjekte).

Type of bower decoration object	Number of times when decoration object was:		Total
	Used during courtship displays	Present but not used	
Green leaf	14	40	54
Petal	0	1	1
Deep Yellow-wood fruit	21	27	48
Other fruit	0	6	6
Black Apple seed	1	10	11
Snail shell	12	22	34
Cicada exuvium	0	10	10
Other exuvium	0	10	10
Piece of blue plastic	5	43	48
	53	169	222

Copulation: The bower display may be terminated at any stage if the female flies away. If, however, the female is ready to copulate, she crouches in the bower avenue in a tilted-forward posture. The male comes around the bower and mounts the female from behind. Copulation takes place in the avenue or directly in front of it, if the female had backed out of the avenue during a forehead-presentation advance of the male. After copulation, the female (but not the male) ruffles up her feathers and shakes them vigorously before flying away.

Arboreal display: During arboreal display, the male perches or slightly crouches on a horizontal branch, c. 30 to 50 cm from the female. The male sings and performs wing flicks and nape presentations similar to those seen in bower display. However, the male remains more stationary in arboreal display, making only short movements of c. 5 to 10 cm. The female appears to directly watch the male only occasionally. When the female hops or flies away, the male often follows and starts another arboreal display on the branch where the female alighted.

Patterns of female visits

During the 1516 hours spent monitoring bower activities (Table 7.1), 77 visits by females were observed. The patterns of female visits at bowers are summarized in Table 7.6. In 58 of the 77 visits (75.3 %; 2a-c in Table 7.6), the female arrived at the bower escorted by the bower-owning male, both individuals flying in together. In the remaining 19 of the 77 visits (24.7 %; 1a-c), the female arrived at the bower on her own, but in most of these cases the male was absent throughout the female's visit (15 out of 19 visits; 1a). A total of 54 courtship displays was observed (1c, 2b and 2c). Most courtship displays (96.3 %) occurred after the female had arrived escorted by the male (52 out of 54 courtship displays; 2b and 2c). Five female visits led to a copulation (2c), all of which were observed after the female had arrived at the bower escorted by the bower-owning male.

Table 7.6. Patterns of female visits at Regent Bowerbird bowers (*n* = 77 visits by females).
Tab. 7.6. Folge von Verhaltensweisen bei Besuchen von Weibchen an Gelbnacken-Laubenvogel-Lauben (*n* = 77 Besuche von Weibchen).

Observed pattern of female visit	Number of visits	Percentage of 77 visits
(1) Female arrives at bower on her own:		
(a) male is absent throughout the female's visit, female leaves	15 visits	19.5 %
(b) male is present but does not start to display, female leaves	2 visits	2.6 %
(c) male is present and starts to display, but female leaves	2 visits	2.6 %
(2) Female arrives at bower escorted by male:		
(a) male does not start to display and female leaves	6 visits	7.8 %
(b) male starts to display, but female leaves	47 visits	61.0 %
(c) male starts to display, copulation takes place	5 visits	6.5 %

Of the five observed copulations, four were seen in 1989, none in 1990 and one in 1991. The four copulations seen in 1989 took place at the same bower and involved the same male but different females, giving the first observational evidence of polygamy in this species. The successful courtship displays that preceded the five observed copulations had a mean duration of 24.5 ± 3.8 minutes (range 20.4-28.8 minutes). The mean duration of courtship displays which did not lead to a copulation was 5.9 ± 6.0 minutes (range 0.1-21.5 minutes). All unsuccessful courtship displays were terminated by the female, who backed out of the avenue and left the bower. No case of disruption of courtship displays by intruding males was observed.

Of the 54 courtship displays observed, 49 (90.7 %) were performed by adult males and 5 (9.3 %) by subadult males. Several colour-banded females were observed visiting more than one bower within one mating season. The durations of the 49 female visits involving a courtship display by an adult male were not correlated with the symmetry of the bower walls (Spearman's rank correlation, $r_s = -0.053$, $n = 49$, $P = 0.715$), the total number of decoration objects ($r_s = -0.073$, $n = 49$, $P = 0.612$), or the number of a certain type of bower decoration ($r_s < 0.2$ and $P > 0.25$ for all types of bower decoration). There was, however, a significant correlation between the rank of the overall quality of the bower construction and the duration of female visits ($r_s = 0.508$, $n = 49$, $P < 0.004$).

7.3.2 Sexual competition

Bower destruction and decoration stealing

During the 1516 hours spent monitoring bower activities (Table 7.1), 114 visits by intruding males were observed, i.e. visits by males other than the bower owner. Of these 114 visits, 62 (54.4 %) involved damage to the bower caused by the intruding male. In 52 of these 62 visits (83.9 %) involving damage, the intruder pulled sticks out of the bower (bower destruction); in 33 visits (53.2 %), the intruder took a decoration object in his bill (see Plate 32) and flew away with it (decoration stealing); 23 visits (37.1 %), all of which were made by adult males, involved both bower destruction and decoration stealing. Bower destruction occurred at a mean rate of 0.034 times per hour and 0.246 times per day, and decoration stealing occurred at a mean rate of 0.022 times per hour and 0.156 times per day.

The selectiveness in decoration stealing is summarized in Table 7.7, which compares the number of times a certain type of decoration was stolen from a bower with the number of times that type of decoration was present but not stolen. Certain types of decoration were not stolen at a frequency corresponding to the frequency of their presence in bowers (6x2 contingency analysis, $\chi^2 = 21.88$, *d.f.* = 5, $P < 0.001$). Two types of decoration were stolen more often than expected from their frequency of presence: pieces of blue plastic ($\chi^2 = 7.94$, *d.f.* = 1, $P < 0.005$) and snail shells ($\chi^2 = 5.85$, *d.f.* = 1, $P < 0.02$). Green leaves were stolen less often than expected from their frequency of presence (χ^2 = 6.12, *d.f.* = 1, $P < 0.02$). These data indicate that intruding males discriminate between types of decoration objects during their decoration stealing.

Table 7.7. Selectiveness in decoration stealing by male Regent Bowerbirds (n = 45 decoration objects stolen).
Tab. 7.7. Auswahlverhalten von männlichen Gelbnacken-Laubenvögeln beim Stehlen von Dekorationsobjekten (n = 45 gestohlene Dekorationsobjekte).

Type of bower decoration object	Number of times when decoration object was: Stolen from bower	Present but not stolen	Total
Green leaf	5	24	29
Deep Yellow-wood fruit	10	23	33
Black Apple seed	0	5	5
Snail shell	13	9	22
Cicada exuvium	0	5	5
Piece of blue plastic	17	12	29
	45	78	123

Intruding males generally arrived at a bower when the owner was not present (in 106 or 93.0 % of the 114 observed visits). Visits by intruders involving damage to the bower tended to be shorter than visits not involving damage (mean durations of 121 ± 125 seconds and 269 ± 369 seconds, respectively), but this difference was not statistically significant (Mann-Whitney *U*-test for large samples, n_1 = 62, n_2 = 52, z = 1.269, P = 0.204).

Observations of bower raiding are summarized in Table 7.8, which lists male bower-visitors and bower owners and gives the ratio of the number of bower visits involving damage to the bower per total number of visits. Of the 114 visits by intruding males, 72 (63.2 %) were made by adult males, and 42 (36.8 %) were made by subadult males. Of the 72 visits by intruding adult males, 49 (68.1 %) involved damage to the bower, but only 13 of the 42 visits by intruding subadult males (31.0 %) involved damage. The proportion of the visits by intruders involving damage was significantly larger in adult males than in subadult males (χ^2 = 14.72, *d.f.* = 1, $P < 0.0002$).

The proportion of visits involving damage to the bower was, however, very different among the individual adult males observed as intruders (Table 7.8). Males RNR, RWN, RWW and NNB caused damage during every visit. Male RRR caused damage in 16 of 17 observed visits. In the remaining visit, RRR arrived at bower 66 when the owner GWW was present; after GWW performed several wing flaps in a bent-forward posture, RRR flew away without causing damage. Males RBN, RGR and RGW, on the other hand, rarely or never caused any damage to the bowers they visited.

Table 7.8. Bower raiding in the Regent Bowerbird. Figures are the number of visits involving damage to the bower (bower destruction and/or decoration stealing) per total number of visits. Figures in brackets below bower owners are the number of bowers found (see Fig. 7.9). Unb. = unbanded owner; Unid. = unidentified visitor; + = male damaged his own bower(s).

Tab. 7.8. Laubenüberfälle beim Gelbnacken-Laubenvogel. Angegeben wird die Anzahl der Besuche mit Laubenbeschädigung (Zerstörung der Laube und/oder Stehlen von Dekorationsobjekten) pro Gesamtzahl der Laubenbesuche. In den Klammern unter den Laubenbesitzern wird die gefundene Anzahl der Lauben pro Individuum angegeben (siehe Abb. 7.9). Unb. = unberingter Laubenbesitzer; Unid. = nicht identifizierter Laubenbesucher; + = Männchen beschädigte seine eigene(n) Laube(n).

Visitor of bower	Owner of bower															Total
	Adult males												Subadult males			
	RRR (3)	RNR (1)	RBN (4)	RGR (2)	RWN (6)	RWW (2)	NRB (1)	NNB (1)	GWW (1)	Unb. (2)	Unb. (2)	Unb. (1)	RGG (2)	NBR (1)	NBN (1)	
Adult:																
RRR	+		3/3		5/5				8/9							16/17
RNR						1/1					3/3	1/1				5/5
RBN	1/5		+										0/1			1/6
RGR	0/1													0/1		0/2
RGW						0/3					0/1					0/4
RWN					+			4/4								4/4
RWW					5/5											5/5
NNB					3/3											3/3
Unid.	2/2			6/15	0/1	0/1				6/6	+	+		1/1		15/26
Subadult:																
RWG					0/3											0/3
NRB			1/4													1/4
NBR				5/12												5/12
NBG					0/4											0/4
NGR				0/2												0/2
GRN	1/2															1/2
Unid.			0/2	3/3		0/4					0/2	2/2	0/1	1/1		6/15
Total:																
Adult	3/8	0/0	3/3	6/15	13/14	1/5	0/0	4/4	8/9	6/6	3/4	1/1	0/1	1/2	0/0	49/72
Subadult	1/2	0/0	1/6	8/17	0/7	0/4	0/0	0/0	0/0	0/0	0/2	2/2	0/1	1/1	0/0	13/42

Movements of intruding males during bower visits

The movements of colour-banded intruding males during their bower visits are shown in Fig. 7.9. All six colour-banded adult males which were observed as intruders causing damage (RRR, RNR, RBN, RWN, RWW and NNB, see Table 7.8), were also observed as bower owners (see Table 7.1). Visits involving damage to the bower were generally made by the males owning the nearest bowers (Fig. 7.9).

Male RGW, on the other hand, who was never found to own a bower in the course of this study, showed maintenance behaviour at two bowers owned by other males (bowers 55 and 61, see Fig. 7.9); RGW was in his first year as adult male during three visits at bower 55, and in his second year as adult male during a visit at bower 61 (see Tables 7.1 and 7.8 and Appendix 3). Male NRB, when in his last year as subadult male (see Appendix 3), showed maintenance behaviour at bower 32 (owned by RBN, see Table 7.1) and caused damage to this bower during only one of his four visits (see Table 7.8). One year later, in his first year as adult male, NRB built a bower (bower 74, see Table 7.1) close to the previous bowers of RBN (see Fig. 7.9), after RBN had disappeared at the end of the third mating season studied.

Rebuilding of bowers and bower-location changes

Bower destruction was observed at twenty of the 33 active bowers monitored during this study. Eight bowers were destroyed but the act of destruction was not observed. Five bowers were not destroyed but disintegrated naturally after the mating season (see Table 7.1). Rebuilding of the bower by its owner was observed at 11 of the 28 destroyed bowers (39.3 %). However, bower owners stopped rebuilding after an intruding male had caused more severe damage.

The only individual that was ever observed to rebuild a completely flattened bower was a subadult male: RGG built a new bower at the location of his previous bower (bowers 58 and 56, respectively), which had been destroyed one and a half months before (see Table 7.1 and Fig. 7.9). In all other cases where a male was observed to build a new bower after his previous bower had been destroyed, the bower location was changed (see Fig. 7.9). The mean distance of twelve bower-location changes of colour-banded adult males was 64.2 ± 54.9 m (range 12.5-190.0 m). A new bower was always built in a different liana thicket than the previous one. All bowers of individual males were located within an area of approximately 0.3-0.8 ha (Fig. 7.9). Males were not observed to change their bower location into, or across, areas containing bowers of other males.

At nine bowers of colour-banded adult males, the owner was observed to destroy his own bower before abandoning it. In eight of these cases, the owner, who had maintained the bower for several days, destroyed his bower after it had been damaged by an intruding male. In the remaining case, adult male RWN destroyed his own bower 72 (see Table 7.1) after it had been visited by an intruder, although the latter did not damage the bower. The damage inflicted on a bower when it was destroyed by its owner was considerably more extensive than the damage caused by intruders. During the three

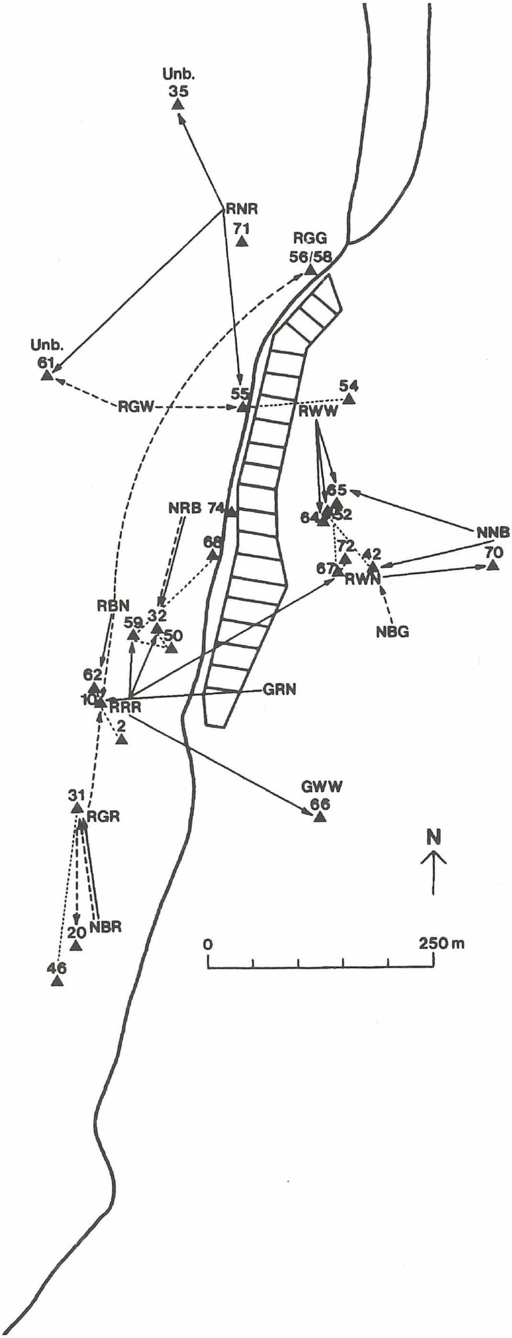

Figure 7.9. Movements during bower visits by male Regent Bowerbirds in the Sarabah Range study area (summary of observations made during the three mating seasons studied). Visits involving damage to the bower are marked as solid lines, visits not involving damage are marked as broken lines. Males are designated by combinations of three letters representing their colour bands; Unb. = unbanded male. Bower-location changes are indicated by dotted lines.

Abb. 7.9. Fortbewegungen bei Laubenbesuchen von männlichen Gelbnacken-Laubenvögeln im Untersuchungsgebiet in der Sarabah-Bergkette (Zusammenfassung von Beobachtungen in den drei untersuchten Paarungssaisons). Besuche mit Laubenbeschädigung sind als durchgezogene Linien markiert, Besuche ohne Laubenbeschädigung als gestrichelte Linien. Die Männchen sind mit Kombinationen aus drei für ihre Farbringe stehenden Buchstaben bezeichnet; Unb. = unberingtes Männchen. Lauben-Standortswechsel sind mit gepunkteten Linien angedeutet.

mating seasons studied, none of the abandoned bower locations of adult males was ever used again for bower building by the same or another individual. Moreover, many of the 42 rudimentary bowers found during this study were probably formerly active bowers (see Chapter 6), but none of them was used again for bower building.

Due to the bower damage caused by intruding males, and due to the subsequent abandoning of bowers by their owners, most active bowers were maintained for only a few days (see Fig. 7.10). Twenty of the 33 active bowers (60.6 %) found during this study were maintained for ten days or less. Only five bowers were maintained for more than 25 days, and four of these bowers were never visited by an intruder (bowers 4, 50, 54 and 57, see Table 7.1).

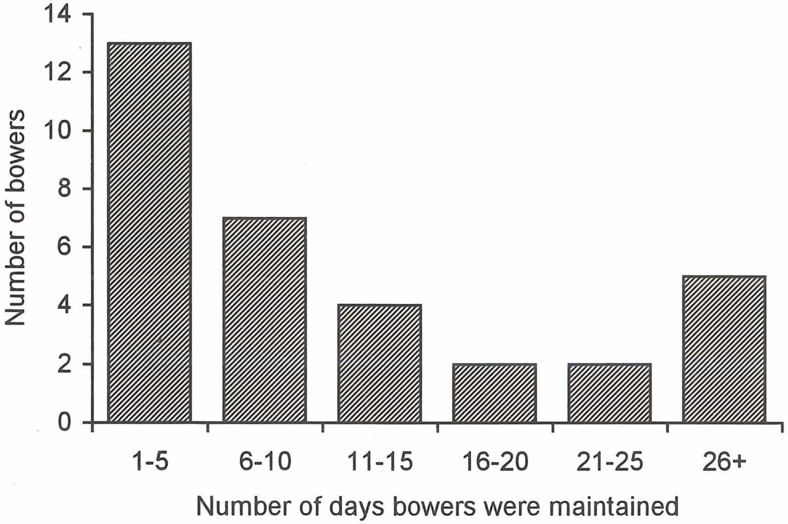

Figure 7.10. Survival of Regent Bowerbird bowers. Number of days active bowers were maintained before being destroyed (*n* = 33 active bowers).

Abb. 7.10. Fortbestand von Gelbnacken-Laubenvogel-Lauben. Anzahl der Tage, die Lauben als Balzplatz genutzt und unterhalten wurden, bevor sie zerstört wurden (*n* = 33 als Balzplatz genutzte und unterhaltene Lauben).

Agonistic interactions

Bower owners were present at their bowers during eight of the 114 observed arrivals of intruding males, and arrived at their bowers during another three visits by intruders. Thus, bower owner and intruding male met during 11 of the 114 visits by intruders (9.6 %). In seven of these eleven cases, the intruder left the bower without discernible interaction between bower owner and intruding male. In the remaining four cases, the intruder left after the owner had performed a courtship display (two visits by subadult males) or several wing flaps in a bent-forward posture (two visits by adult males). Only once was the owner observed to chase an intruding male (after he had performed several wing flaps at the intruder).

The observations of agonistic interactions at an artificial feeding site are summarized in Table 7.9. The interactions were usually initiated by an individual hopping towards another individual with its folded wings raised and bill wide open; occasionally, wing flaps in bent-forward posture were performed. The individual that had initiated an interaction was dominant in 346 of the 348 encounters (99.4 %) listed in Table 7.9, and retreated in only two encounters (0.6 %). Another 15 interactions did not have a clear outcome and were omitted from Table 7.9.

Table 7.9. Agonistic interactions of Regent Bowerbirds at an artificial feeding site (n = 348 aggressive encounters). 'Brown' male = immature or subadult male.
Tab. 7.9. Agonistische Interaktionen von Gelbnacken-Laubenvögeln an einer Futterstelle (n = 348 aggressive Begegnungen). 'Brown' male = immatures oder subadultes Männchen.

Dominant individual	Retreating individual			Total
	Female	'Brown' male	Adult male	
Female	138	47	116	301
'Brown' male	2	3	7	12
Adult male	3	4	28	35
Total	143	54	151	348

Of the 348 aggressive encounters summarized in Table 7.9, 306 encounters (87.9 %) involved females. In 301 of these 306 encounters (98.4 %), the dominant individual was a female. Females were occasionally observed fighting, striking each other with their feet. When one female managed to wrap her claws around the legs of the other female, she pecked at the other female until the latter managed to free herself. This type of fighting was never observed among males.

Compared with females, aggressive encounters among males were rare. Most of the observed encounters were interactions among adult males (28 or 66.7 % of 42 encounters). The number of observed interactions among males was too small to assess the relative dominance of individual males. However, in 28 encounters observed among adult males, the dominant individual was known to own a bower in 26 cases, and the retreating individual was known to own a bower in 17 cases. Therefore, most adult males involved in aggressive encounters were bower owners, and adult males which were not known to own a bower were significantly more often the retreating individual than the dominant ($\chi^2 = 8.114$, $d.f. = 1$, $P < 0.005$).

7.4 Discussion

Mating behaviour

The mating behaviour of the Regent Bowerbird shows many similarities to other bowerbirds, but also some striking differences. The observation that bowers of Regent Bowerbirds are generally maintained by a single male (Table 7.1) contrasts with some assertions in the popular literature (SCHODDE & TIDEMANN 1990; LINDSEY 1992) stating that Regent Bowerbird bowers are attended by several males, unlike the bowers of other species.

Most of the postures which male Regent Bowerbirds adopt during their sexual display resemble those of other bowerbird species, particularly those building avenue bowers (for illustrations see GILLIARD 1959, 1963, 1969; WARHAM 1962; COOPER & FORSHAW 1977; VESELOVSKÝ 1978, 1979; COATES 1990). For example, the nape-presentation posture of male Regent Bowerbirds (Fig. 7.4) is nearly identical with the crest-presentation postures of *Chlamydera* males (see WARHAM 1957, 1962; GILLIARD 1959; COOPER & FORSHAW 1977; VESELOVSKÝ 1978, 1979; FRITH & FRITH 1989, 1991; COATES 1990). Such crest-presentation postures are also adopted by male Yellow-breasted and Fawn-breasted Bowerbirds, although males of these species do not possess a bright crest (GILLIARD 1959; DICZBALIS 1974; PECKOVER & FILEWOOD 1976; FRITH & FRITH 1989; COATES 1990). This has been considered as evidence supporting the 'transferral effect' hypothesis (see Chapter 1), as 'crest' presentations in crestless species appear to represent vestigial movements (GILLIARD 1959, 1963, 1969; FRITH & FRITH 1989, 1991).

The colourful wings of male Regent Bowerbirds may be more important in their sexual display (Figs 7.3 and 7.6-7.8) than the dull wings of other bowerbird species in their respective displays, but wing flicks have also been observed as a display element of bowerbirds with cryptic plumage (COOPER & FORSHAW 1977; BORGIA 1995a; C.B. FRITH & D.W. FRITH in litt.). Unfortunately, the display of the Regent Bowerbird cannot be compared with congeneric Flame and Fire-maned Bowerbirds, as the displays of the latter are unknown (COATES 1990).

Male Regent Bowerbirds differ markedly from males of other bowerbird species in their low level of time investment in bower attendance: only 3.2 % of daylight hours in adult males (Table 7.3, Fig. 7.1). DONAGHEY (1981) found that male Satin Bowerbirds spent an average of 17.2 % of daylight hours at or near their bowers; VESELOVSKÝ (1978, 1979) found that a male Great Bowerbird spent 28.5 % of daylight hours at his bower while building it, and 47.2 % of daylight hours at the peak of the mating season; PRUETT-JONES & PRUETT-JONES (1982) found that the bower attendance of male Macgregor's Bowerbirds averaged 54 % of daylight hours; and FRITH & FRITH (1994b) found that court attendance levels by male Tooth-billed Bowerbirds during the peak activity of a display season can be up to more than 80 % of daylight hours. Male Regent Bowerbirds also spent much less time vocalizing than males of other species that regularly produce loud advertisement calls (DONAGHEY 1981; DIAMOND 1982a, 1987; PRUETT-JONES &

PRUETT-JONES 1982, 1983; FRITH 1989; FRITH & FRITH 1994b, 1998a). Low levels of time investment in bower attendance similar to male Regent Bowerbirds were, however, found in males of the congeneric *Sericulus* species: P.D. DWYER and M. MINNEGAL (in COATES 1990) found 5.9 % of daylight hours in the Flame Bowerbird, and MACKAY (1989 and pers. comm.) found less than 1 % in the Fire-maned Bowerbird.

DONAGHEY (1981) observed male Satin Bowerbirds spending 73 % of daylight hours within 50 m of their bowers when he watched them from towers, though they were visible from ground hides over only 17.2 % of daylight hours. It is possible that the male Regent Bowerbirds observed in this study spent a certain part of the day close to their bowers but invisible from the ground hides. However, this does not contradict the finding that they spent considerably less time at their bowers than males of other species because all figures given above were determined from ground hides. The observation that male Regent Bowerbirds generally departed from their bowers by flying away rapidly also suggests that they were not close to their bowers over most of the day. This view is furthermore supported by the results of the radio-tracking of a bower-owning adult male. Male Regent Bowerbirds range widely and appear to have relatively large, overlapping home ranges.

Bower-owning subadult male Regent Bowerbirds spent more time at their bowers than adult males (Table 7.4) but still much less time than males of other species. The age-related differences in time budgets, especially the much higher investment in bower building and in solitary display, and the fact that adult males display to younger males in female plumage, suggest that experience and learning are important in the development of the bower-building and display abilities of a male (see VELLENGA 1970, 1986; DONAGHEY 1981; DIAMOND 1982b, 1986a,b; PRUETT-JONES & PRUETT-JONES 1983; BORGIA 1986a, 1993; COLLIS & BORGIA 1992, 1993).

Bower-owning male Macgregor's and Golden Bowerbirds have been observed to cache fruit in the vicinity of their bowers, a behaviour that may assist them in extending the amount of time they spend at their bowers, through reducing the amount of time they must be absent to search for food (PRUETT-JONES & PRUETT-JONES 1985; FRITH 1989; FRITH & FRITH 1998a). This behaviour has not been observed in the Regent Bowerbird, which has a much lower rate of bower attendance.

In species with emancipated males, the males should be selected to maximize their time investment in mate acquisition activities (DONAGHEY 1981; PRUETT-JONES & PRUETT-JONES 1982; LILL 1986; SUTHERLAND 1987). Therefore, the low levels of time investment in display-site attendance of male Regent Bowerbirds and congeneric Flame and Fire-maned Bowerbirds are remarkable. However, the observed patterns of female visits at Regent Bowerbird bowers (Table 7.6) indicate that the initial interaction between male and female does not take place at bowers, in contrast to other bowerbird genera. Instead, most courtship displays, including all successful displays that led to a copulation, were observed after the female had arrived at the bower escorted by the bower-owning male.

Regent Bowerbirds and their congeners live in dense forests and build the smallest bowers of the avenue type (see Chapter 6). The data presented here suggest that the initial interaction between male and female usually takes place in the canopy, where males encounter females more often than at their small, concealed bowers on the forest floor. However, although males may also display to females in the canopy, copulation only takes place after an extended display at the bower, as indicated by the lower intensity of arboreal displays compared with displays at bowers.

The four copulations observed at the same Regent Bowerbird bower during the 1989 mating season gave the first observational evidence of polygamy and skewed male mating success in this species. The small number of copulations observed during this study (only five copulations during 1516 hours of hide observations at 33 active bowers) is not unusual: PRUETT-JONES & PRUETT-JONES (1982, 1983) saw only one copulation during more than 1000 hours of hide observations at bowers of Macgregor's Bowerbird; FRITH (1989) did not see a single copulation during several hundred hours of observations at Golden Bowerbird bowers.

Large numbers of copulations were, however, recorded when bowers of Satin, Spotted and Great Bowerbirds were monitored simultaneously with an infrared-controlled camera system (BORGIA 1985a, 1986a, 1995a,b). Compared with the bowers of Satin, Spotted and Great Bowerbirds, those of the Regent Bowerbird are very difficult to find (see Chapter 6), are maintained for only a small number of days (Fig. 7.10), their locations are frequently changed (Fig. 7.9), and only few bowers are active simultaneously (Table 7.1). It is, therefore, unlikely that a camera monitoring system could be as useful in studying Regent Bowerbirds as it was in the work on other bowerbird genera.

According to PRUETT-JONES & PRUETT-JONES (1983, pp. 50-51), a low rate of copulations during bower observations could suggest "that females visit numerous males on repeated occasions throughout the long display period before choosing a mate". The small number of copulations observed during this study could also be related to the unusual drought conditions during the second and third field seasons (see Chapter 2), which could have led to a generally poor reproductive success in these years (see Chapter 5). However, in accordance with the suggestion of PRUETT-JONES & PRUETT-JONES (l.c.), several colour-banded female Regent Bowerbirds were observed visiting more than one bower within a mating season, giving evidence that females are free to sample several males, a requirement for the occurrence of female choice (BRADBURY & DAVIES 1987; HARVEY & BRADBURY 1991).

The correlation between the rank of the overall quality of Regent Bowerbird bower-constructions and the duration of female bower-visits gave the first evidence of an effect of bower quality on the mate-choice decisions of female Regent Bowerbirds. This result resembles the patterns of female preferences for males with well-constructed bowers found in Satin Bowerbirds (BORGIA 1985a) and in Spotted Bowerbirds (BORGIA & MUELLER 1992; BORGIA 1995b).

That the symmetry of Regent Bowerbird bower-walls was not correlated with the duration of female visits appears to contradict the correlation between bower quality and female preference. This may have been caused by the way bower symmetry was quantified: the measured differences in height and width of the bower walls may be less important in affecting female choice than the general appearance of the bower avenue and the inside of the bower walls. Females usually sit in the avenue or in an entrance of it during bower displays (Fig. 7.6), and they may not notice asymmetrical outer dimensions of a bower while watching the male.

Bower-owning male Regent Bowerbirds regularly paint the inside of the bower walls, just as males of other species building avenue bowers do (GANNON 1930; NUBLING 1939; MARSHALL 1954; BELL 1967; GILLIARD 1969; PECKOVER 1970; COOPER & FORSHAW 1977; FRITH & FRITH 1989, 1998a; COATES 1990). The observation that most painting is done in the early hours of the morning, earlier than most courtship displays (Fig. 7.1), suggests that painting may be important in influencing female mating preferences.

That the numbers of decoration objects in Regent Bowerbird bowers were not correlated with the duration of female visits could explain the fact that the number of decorations is very small compared with avenue bowers of other species (see Chapter 6). Though Regent Bowerbird males always use some decoration objects in their courtship displays (Fig. 7.2, Table 7.5), they do not benefit from owning a larger number of decorations if the number of objects is not correlated with female preferences.

But, if the mating success of male Regent Bowerbirds is correlated with the quality of their bower constructions, why has female choice not produced more elaborate bowers in this species? The mean duration of courtship displays that preceded a copulation was a remarkable 24.5 minutes. Successful courtship displays of Regent Bowerbirds are, therefore, several times longer than successful courtships in other bowerbird species (G. BORGIA pers. comm.). This suggests that the display performance of male Regent Bowerbirds may be of particular importance for their mating success, possibly more so than in other bowerbird species in which more complex bowers may have led to reduced courtship time. It is, however, unknown which parameters of the very complex courtship display of male Regent Bowerbirds may be linked to their mating success. There are only few studies where, after many years of extensive research, correlations between display parameters and mating success were found (e.g. GIBSON & BRADBURY 1985; GIBSON et al. 1991). Another important constraint on the selection of more elaborate bower constructions in Regent Bowerbirds are the patterns of male-male competition in this species.

Sexual competition

The patterns of male interactions in the Regent Bowerbird are similar to those of other bowerbird species: males destroy bowers of other males and steal decoration objects from them (Tables 7.7-7.8). Most bower raiding is directed at bowers of the nearest neighbours (Fig. 7.9), the most likely sexual competitors (see PRUETT-JONES & PRUETT-JONES 1983; BORGIA 1985b; BORGIA & GORE 1986).

Intruding males discriminate between types of decoration objects in their decoration stealing: pieces of blue plastic were stolen more often than expected from their presence in bowers (Table 7.7), but they were used less often in courtship displays (Table 7.5). Similar observations have been made in Satin Bowerbirds: rare objects are often stolen but rarely held by males during courtship displays (BORGIA 1985a; BORGIA et al. 1985; BORGIA & GORE 1986).

An interspecific comparison of the rates of bower destruction and decoration stealing (see Table 7.10) reveals that bower raiding occurs more often in Regent Bowerbirds than in three other species building avenue bowers, Satin, Spotted and Great Bowerbirds, and less often than in the maypole-building Macgregor's Bowerbird. The highest rates of decoration stealing have been found in the Tooth-billed Bowerbird with its aggregated display sites. These differences show an inverse correlation between the frequency of bower raiding and nearest-neighbour distances (see Chapter 6): bower raiding occurs less often in species with larger interbower distances (see BORGIA & MUELLER 1992).

Table 7.10. Interspecific comparison of the mean rates of bower destruction and decoration stealing (per bower).

Tab. 7.10. Interspezifischer Vergleich der durchschnittlichen Häufigkeit von Laubenzerstörung und Stehlen von Dekorationsobjekten (pro Laube).

Bowerbird species	Mean rate of bower destruction	Mean rate of decoration stealing	References
Tooth-billed Bowerbird	Not applicable	0.38* per day (1979) 0.88* per day (1980)	1 1
Macgregor's Bowerbird	0.10 per hour 1.20 per day	Not seen	2
Regent Bowerbird	0.034 per hour 0.246 per day	0.022 per hour 0.156 per day	3
Satin Bowerbird	0.12 per day 0.2 per day	0.11** per day ?	4,5 6
Spotted Bowerbird	0.002 per hour (1987) 0.012 per day (1987) 0.032 per day (1989)	0.004 per hour (1987) 0.024 per day (1987) ?	7 7 6,8
Great Bowerbird	? per hour 0.094 per day	in between Satin and Spotted Bowerbird	6

References: 1 = FRITH & FRITH 1994b; 2 = PRUETT-JONES & PRUETT-JONES 1982; 3 = this study; 4 = BORGIA 1985b; 5 = BORGIA & GORE 1986; 6 = BORGIA 1995a; 7 = BORGIA & MUELLER 1992; 8 = BORGIA 1995b. * = rate of leaf stealing; ** = rate of feather stealing.

According to PRUETT-JONES & PRUETT-JONES (1994, p. 607), a series of game-theory models developed to examine "costs and benefits of alternative behaviour patterns in terms of access to females" demonstrated that, "under most circumstances, strategies of marauding bowers and/or stealing decorations are stable against a strategy of guarding bowers and not disrupting". The strategy of guarding bowers was stable only "if intruders had to travel long distances between bowers or if residents were able to quickly repair damaged bowers" (PRUETT-JONES & PRUETT-JONES l.c.).

In the Regent Bowerbird, decoration stealing was observed less often than bower destruction (Table 7.10). This difference may be related to the small number of decoration objects found in their bowers (see Chapter 6). Stealing has not been observed in Macgregor's Bowerbird which uses few large decoration objects (PRUETT-JONES & PRUETT-JONES 1982, 1994; DIAMOND 1982a,b; BORGIA & GORE 1986; COATES 1990).

The comparatively small proportion of visits involving bower destruction and/or decoration stealing among the bower visits by subadult male Regent Bowerbirds (Table 7.8), and the described observations of the males RGW and NRB, gave evidence of behavioural differences between individual males. Most active bowers are maintained by adult males (Table 7.1), whereas subadult males and males in their first year(s) as adult male may adopt alternative mating tactics and show satellite behaviour (ARAK 1984; DOMINEY 1984). Similar observations have been made on other bowerbird species (BORGIA & MUELLER 1992).

While the males of most bowerbird species usually rebuild bowers which have been damaged by intruders (MARSHALL 1954; VELLENGA 1970; PRUETT-JONES & PRUETT-JONES 1982, 1983; FRITH & FRITH 1989; BORGIA & MUELLER 1992), male Regent Bowerbirds were observed to reconstruct their bowers only after minor damage. Instead, bower raiding in the Regent Bowerbird frequently led to an abandoning of the bower by its owner, and to a shift in the individual's bower location (Fig. 7.9). These observations confirm BELL's (1970) suggestion that Regent Bowerbird males (and possibly also males of the congeneric Flame and Fire-maned Bowerbirds) maintain their bowers for a very short time only (Fig. 7.10), in sharp contrast to the strong bower-site fidelity found in other genera (e.g. VELLENGA 1980b; DIAMOND 1987; CROME & MOORE 1989; FRITH 1989; COATES 1990; FRITH & FRITH 1998a).

The frequency of bower-location changes in Regent Bowerbirds may explain the abundance of rudimentary bowers in this species (see Chapter 6). Bower-location changes do also occur in other species (HOPKINS 1974; DONAGHEY 1981; C.B. FRITH & D.W. FRITH in litt.), but far less often. For example, more than half of the Satin Bowerbird bowers observed by DONAGHEY (1981) were built on the site already used during the previous mating season, and bower-location changes averaged a distance of less than 10 m. In contrast, none of the abandoned bower locations of adult male Regent Bowerbirds was ever used again during the three mating seasons studied, and the bower-location changes averaged more than 60 m.

This striking difference in bower-site fidelity between Regent Bowerbirds and other bowerbird species is probably related to the differences in their bower structures and time investment in bower attendance. In contrast to the males of other species, bower-owning adult male Regent Bowerbirds spend only a very small percentage of daytime at their bowers (Table 7.3). The probability that a bower owner is present at his bower when an intruder is visiting it is very low; thus, the probability that a bower owner can defend his bower against an intruder is also very low. It takes a Regent Bowerbird male only a few hours to build a new bower (see Chapter 6), whereas males of other species require several days or even weeks to build one of their considerably larger bowers (MARSHALL 1954; GILLIARD 1969; PECKOVER 1970; COOPER & FORSHAW 1977; VESELOVSKÝ 1978, 1979; PRUETT-JONES & PRUETT-JONES 1983; COATES 1990). Therefore, it may be more profitable for a Regent Bowerbird male to abandon a bower that has been discovered and damaged by an intruder, and to build a new bower at a new location, instead of rebuilding the old one, which is likely to be revisited by the intruder.

It is possible that Regent Bowerbird males, unlike males of other bowerbird species, are often unaware of the precise location of bowers of their neighbouring competitors. Two findings support this view: (a) four of the five bowers that were maintained for more than 25 days were never visited by any intruders, and (b) none of the 54 observed courtship displays was disrupted by an intruder. In contrast, the disruption of courtship displays has been observed regularly in several other bowerbird species (see MARSHALL 1954; DONAGHEY 1981; PRUETT-JONES & PRUETT-JONES 1982; BORGIA 1986a, 1995a,b), despite the fact that nearest-neighbour distances are greater in most of them (see Chapter 6).

Once a Regent Bowerbird bower has been discovered by an intruding male, it may be worthless to the owner who cannot defend a bower that he only attends for a few minutes each day. A male that continued to escort females to a bower that had been discovered by an intruder would risk finding his bower damaged when he arrived with a female. Female preference for males with well-constructed bowers would favour a male that abandons a bower that has been discovered and damaged by an intruder, and builds a new bower.

But why should a male destroy his own bower before abandoning it, as observed at nine bowers of colour-banded adult males? It may be that a male that abandons his bower without previously destroying it risks the bower being taken over by one of the males showing satellite behaviour. VELLENGA (1970) observed that adult male Satin Bowerbirds dismantled their bowers before dispersing at the end of the mating season.

Despite the frequency of bower raiding in the Regent Bowerbird, direct aggressive encounters of males were observed only rarely, even when bower owner and intruder met. Bower-owning Satin Bowerbirds vigorously expel intruders from their bowers (DONAGHEY 1981; BORGIA 1986a). While DONAGHEY (1981) did not observe agonistic interactions of male Satin Bowerbirds away from their bowers, BORGIA (1985b) observed such interactions at feeding sites, and used these as a measure of male dominance. Among adult male Regent Bowerbirds, most individuals dominant in aggressive encounters were bower owners, while individuals not known to own a bower retreated significantly more often than were dominating. These observations suggest that male dominance is important for the ability of an individual to hold a bower (see BORGIA 1985b; BORGIA & MUELLER 1992), even though active defence of a territory around the display site is less obvious than one might expect (DAVIES 1991).

The spacing of Regent Bowerbird bowers (see Chapter 6) appears largely to be the result of bower raiding and subsequent bower-location changes. While all bowers of a particular male were located within a relatively small area of less than 1 ha (Fig. 7.9), the radio-tracking data suggest that bower-owning adult males make excursions in a much larger area, encompassing bower sites of several other males. Faithfulness to a home range and high annual survival rates (see Chapter 5) may assist individual males in successful siting of bowers.

The observation that agonistic interactions are much more common among females than among males (Table 7.9) may explain the reversed sexual size dimorphism of the Regent Bowerbird (see Chapter 3). The observation that males only rarely met at bowers suggests that male-male competition may involve direct aggressive encounters less often than competition among females.

8 Breeding Biology and Parental Behaviour

8.1 Introduction

In promiscuous species, male and female individuals only come together for mating and do not develop any pair bond (FORD 1989; DAVIES 1991). Promiscuity has been found in many frugivorous passerines (SNOW 1971, 1982; LILL 1975; BEEHLER 1987; BROOKE & BIRKHEAD 1991). These birds may often forage in groups containing both sexes, at least outside the breeding season, but do not show any close bond between individuals. Nest-building, brooding, feeding and parental defence are performed solely by the female. The male is emancipated from all parental care and only contributes sperm.

This type of parental behaviour, where females provide uniparental brood care, is shown by most species in the bowerbird family. Males of all species which clear courts and/or build bowers have never been observed to provide any parental care; only in catbirds *Ailuroedus* spp., the only monogamous genus in the bowerbird family (see Chapter 1), is parental care provided by both sexes (DONAGHEY 1981; PRUETT-JONES & PRUETT-JONES 1982; DONAGHEY et al. 1985; FRITH & FRITH 1985b, 1988, 1989, 1990a,c, 1994a, 1998a,b; DIAMOND 1986b; FRITH 1989; COATES 1990).

A comparison of biparental Green Catbirds and uniparental Satin Bowerbirds by DONAGHEY (1981) revealed similarities in some aspects of their breeding biology, and differences in others. Both species had a typical clutch size of two and were also similar in their incubation and nestling periods. Nest attentiveness and nesting success, however, were greater in Green Catbirds than in Satin Bowerbirds. Although adults of both species are largely frugivorous (see Chapter 4), fruit only predominated in the nestling diet of Green Catbirds, whereas nestlings of Satin Bowerbirds were mainly fed on insects (DONAGHEY 1981).

Food availability is considered as the major ultimate factor in determining the breeding season: birds generally breed when food required for rearing young is most abundant (MARSHALL 1951b; LACK 1954; FORD 1989; BEZZEL & PRINZINGER 1990; BROOKE & BIRKHEAD 1991). Timing and duration of the breeding season, in turn, influence mating opportunities: where females are highly synchronized in their periods of sexual receptivity, there is little potential for individual males to have multiple mating success (EMLEN & ORING 1977; ORING 1982). Data on breeding attempts of several bowerbird species suggest that their egg-laying is sufficiently asynchronous to provide multiple mating opportunities for individual males (CAMPBELL 1900; NORTH 1901-1904; BERULDSEN 1980; DONAGHEY 1981; DONAGHEY et al. 1985).

In the Regent Bowerbird, the first observations of uniparental female brood care were made by GILBERT (1910, 1913), JACKSON (1914) and CHAFFER (1932). Due to the activities of egg collectors, for decades nests of Regent Bowerbirds were found considerably more often than their bowers (MARSHALL 1954). In contrast, the main emphasis of the field work for this study has been on finding Regent Bowerbird bowers (see Chapters 6 and 7), while only few nests were discovered. However, the data of egg collectors and other observations on the breeding of this species have not been previously summarized.

All available information on breeding biology and parental behaviour of the Regent Bowerbird shall be examined in this chapter, in order to complete the picture of the reproductive biology and evolutionary ecology of this species. In particular, timing and duration of the period of egg-laying shall be analysed to consider the degree of synchronization in female receptivity, and characteristics of the nesting ecology shall be compared with other bowerbird species.

8.2 Materials and methods

Only three Regent Bowerbird nests were discovered during the field work in the Sarabah Range. The extremely time-consuming search for bowers and their monitoring prevented a more extensive search for nests, which are difficult to find. More data on breeding biology and parental behaviour of the Regent Bowerbird were obtained from egg collectors' notebooks and egg shells kept in oological collections, and from the literature.

Egg shells and accompanying notes were examined in the following collections (in alphabetical order): Australian Museum, Australian National Wildlife Collection, British Museum (Natural History), Museum of Victoria (H.L. White Collection and L. Harvey Collection), Queensland Museum, South Australian Museum (including Morton-Oakley Collection and Capt. S.A. White Collection), Western Foundation of Vertebrate Zoology, and Zoologisches Museum Berlin.

Further data and descriptions were taken from GOULD (1865), CAMPBELL (1900), NORTH (1901-1904), GILBERT (1910, 1913), LE SOUEF (1913), JACKSON (1914), CHAFFER (1932, 1984 and pers. comm.), BROWN (1956), BELL (1960), BERULDSEN (1980 and in litt.), SINDEL (1989 and pers. comm.) and the RAOU Nest Record Scheme of the Royal Australasian Ornithologists Union.

Together, these sources constituted data of 155 breeding attempts of Regent Bowerbirds. Sample sizes of certain aspects of the breeding biology were, however, well below this figure because the amount of information differed greatly among the records of breeding attempts.

Egg collectors endeavoured to collect clutches as soon as these were complete (see LONGMORE & BOLES 1989). Therefore, the dates on the labels in egg collections were taken as the dates when breeding attempts were initiated. These dates were used to study timing and duration of the period of egg-laying. When the number of incubation days was given on a label, the date that the clutch had been completed was calculated by subtracting the number of incubation days.

Geographical trends in the timing of the period of egg-laying were analysed to consider important factors in determining the breeding season. Breeding attempts were separated into attempts of southern and of northern populations. The basis for this separation was the line of equal summer/winter moisture index. This line divides the Australian continent into a northern part where precipitation peaks in summer, and a southern part where precipitation peaks in winter; the 'moisture index' is the ratio of estimated actual to potential evapotranspiration (see NIX 1981). The line of equal summer/winter moisture index crosses north-eastern New South Wales along the line Stanthorpe-Grafton approximately (see ADAM 1987). Nesting locations to the south of this line were assigned to the southern populations, and nesting locations north of this line were assigned to northern populations.

As indices of the variation in size and shape of eggs, their length, l, and maximum breadth, b, were measured with calipers. Egg volume, V, was estimated from these linear egg dimensions using the formula

$$V = K_V \cdot l \cdot b^2$$

where K_V is a volume coefficient, a function of the egg shape. Based on PRESTON (1974), DONAGHEY (1981) and FRITH & FRITH (1985b) used $K_V = \pi : 6$ to estimate egg volumes of bowerbird species because a bowerbird egg is essentially a prolate ellipsoid in shape. According to HOYT (1979), the volumes of most bird eggs can be estimated within 2 % using $K_V = 0.51$. Estimates of the volume of Regent Bowerbird eggs were calculated using both values of K_V. Fresh egg mass was estimated from the volume estimates by multiplying egg volume by an assumed specific gravity of 1.05 g/cm^3 for egg contents (BERGTOLD 1929).

8.3 Results

Timing and duration of the period of egg-laying

Data of breeding attempts of the Regent Bowerbird came from most parts of its range, with the exception of the northernmost part of the range (Clarke Range to Blackall Range; see Chapter 3). Egg-laying and incubation were initiated from the end of September until the end of January. Both the earliest and the latest clutch ever discovered were found in 1909: the earliest was found on 20 September (near the lower Clarence River in north-eastern New South Wales, AM O.51393), the latest was found on 25 January (at Coolabunia near Kingaroy in south-eastern Queensland, MVHLW 866C). According to these data, the maximum duration of the period of egg-laying in the wild is four months. In captivity, an infertile egg was laid later, on 9 February 1987 (in Sydney, SINDEL 1989).

Timing and duration of the period of egg-laying of southern and northern populations are shown in Fig. 8.1, in which data of breeding attempts were assigned to half-month periods. In both southern and northern populations the period of egg-laying had a duration of approximately four months. The timing of the period of egg-laying was, however, different between southern and northern populations: breeding attempts in southern populations were initiated significantly more often in earlier half-month periods than breeding attempts in northern populations (Student's *t*-test, $t = 2.734$, *d.f.* = 135, $P < 0.01$).

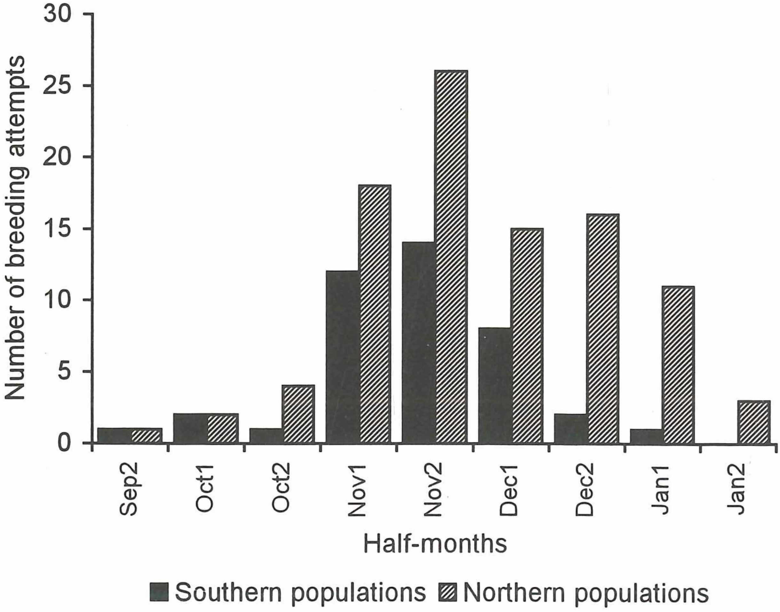

Figure 8.1. Timing and duration of the period of egg-laying of southern and northern populations of the Regent Bowerbird. Breeding attempts at locations south of the line of equal summer/ winter moisture index were assigned to the southern populations ($n = 41$), breeding attempts at locations north of this line were assigned to the northern populations ($n = 96$). Data of breeding attempts were assigned to half-month periods.

Abb. 8.1. Zeitpunkt und Dauer des Zeitraums der Eiablage von südlichen und nördlichen Populationen des Gelbnacken-Laubenvogels. Brutversuche an Stellen südlich der Linie in Sommer und Winter identischen Feuchtigkeitsindexes wurden den südlichen Populationen zugeschrieben ($n = 41$), Brutversuche an Stellen nördlich dieser Linie wurden den nördlichen Populationen zugeschrieben ($n = 96$). Die Daten der Brutversuche wurden Zeiträumen von je einem halben Monat zugeteilt.

The largest sample of breeding attempts discovered in a single locality was found in the Big Scrub area in north-eastern New South Wales (Figs 8.2-8.3), where a total of 75 breeding attempts was discovered. All Big Scrub breeding attempts except for one were initiated from mid October until mid January (see Fig. 8.2). Thus, the period of egg-laying in this locality was slightly shorter than in the entire range of the species, but egg-laying still extended over a period of three months.

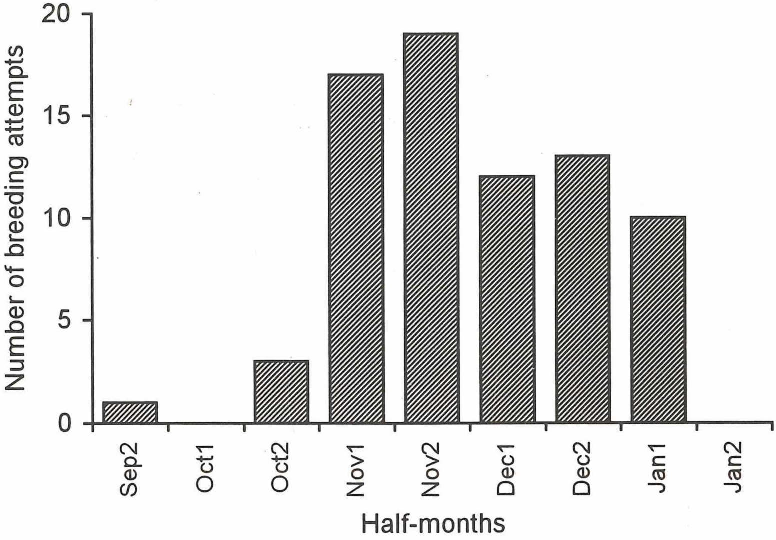

Figure 8.2. Timing and duration of the period of egg-laying of Regent Bowerbirds in the Big Scrub area in north-eastern New South Wales (*n* = 75 breeding attempts). Data of breeding attempts were assigned to half-month periods.
Abb. 8.2. Zeitpunkt und Dauer des Zeitraums der Eiablage von Gelbnacken-Laubenvögeln im Big-Scrub-Gebiet im nordöstlichen Neusüdwales (*n* = 75 Brutversuche). Die Daten der Brutversuche wurden Zeiträumen von je einem halben Monat zugeteilt.

In three breeding seasons (1905, 1906 and 1908), more than a dozen Regent Bowerbird nests were discovered in the Big Scrub area, and allowed a year-by-year comparison of the seasonality of egg-laying (see Fig. 8.3). In these three breeding seasons, all breeding attempts except for one were initiated from the beginning of November until mid January. Therefore, in separate years the period of egg-laying in the Big Scrub area extended over at least two and a half months.

Nests and nest-site characteristics

Nests had a frail, shallow, slightly concave, saucer-shaped structure (see photographs in CAMPBELL 1900; NORTH 1901-1904; CHAFFER 1932, 1984; DISNEY & LANE 1971; DISNEY 1974; THRELFO 1985). The external nest material were rather loosely constructed dry

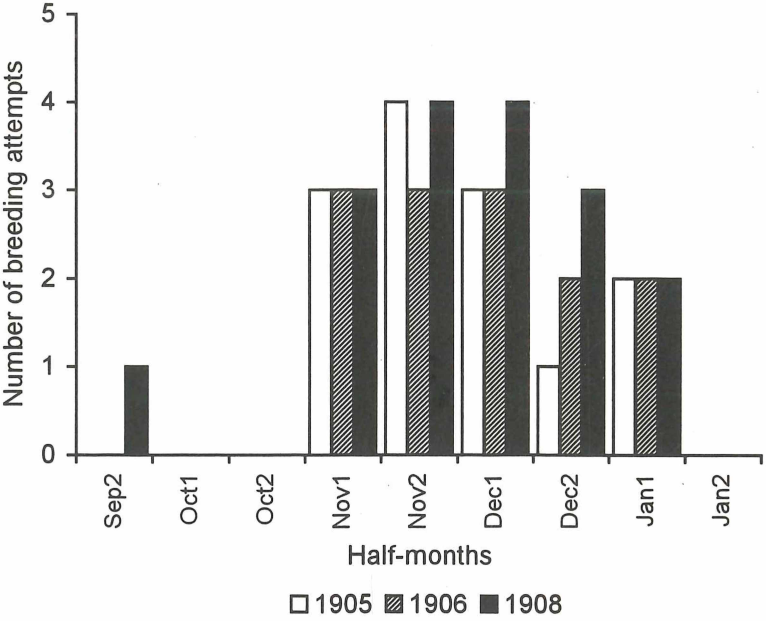

Figure 8.3. Timing of the initiation of breeding attempts of Regent Bowerbirds in the Big Scrub area in north-eastern New South Wales in the breeding seasons 1905 (*n* = 13), 1906 (*n* = 13) and 1908 (*n* = 17). Data of breeding attempts were assigned to half-month periods.
Abb. 8.3. Zeitpunkt des Beginns von Brutversuchen von Gelbnacken-Laubenvögeln im Big-Scrub-Gebiet im nordöstlichen Neusüdwales in den Brutsaisons 1905 (*n* = 13), 1906 (*n* = 13) und 1908 (*n* = 17). Die Daten der Brutversuche wurden Zeiträumen von je einem halben Monat zugeteilt.

sticks. The lining was made of finer twigs and, occasionally, some leaves. Mean nest dimensions were 24.4 ± 5.3 cm external diameter (*n* = 5), 10.8 ± 1.1 cm internal diameter (*n* = 3) and 4.0 ± 0.4 cm depth (*n* = 3).

Nests were built and attended solely by the female. The nest-building period lasts about one to two weeks, as is indicated by the following observations: H.R. ELVERY observed a female building a nest at the beginning of November 1896 and saw at least one egg in this nest on 16 November 1896 (CAMPBELL 1900); GILBERT (1913) discovered a female commencing a nest on 12 November 1911, observing a recess time of three minutes between nest-building visits, and found one fresh egg in this nest on 26 November 1911; C.A.C. CAMERON saw a female carrying a stick to a nest site on 7 December 1968 and observed the female brooding tightly one week later, on 14 December 1968, and collected one freshly incubated egg (QM O.22174).

The incidence of nesting in different plant species is summarized in Table 8.1. In rainforests, Regent Bowerbirds nested in a variety of tree and shrub species. In wet sclerophyll forests, nests have often been located in tea trees *Melaleuca* sp. and wattles *Acacia* sp., two common genera in this type of habitat.

Table 8.1. Incidence of Regent Bowerbird nests in different plant species, arranged in taxonomic order (*n* = 30 nests).
Tab. 8.1. Vorkommen von Gelbnacken-Laubenvogel-Nestern in verschiedenen Pflanzenarten, angeordnet in der Reihenfolge der Systematik des Pflanzenreichs (*n* = 30 Nester).

Plant species	Botanical family	Number of nests
Araucaria bidwillii	Araucariaceae	2
Casuarina sp.	Casuarinaceae	2
Ficus sp.	Moraceae	2
Dendrocnide sp.	Urticaceae	1
Capparis sp.	Capparaceae	3
Acacia sp.	Mimosaceae	5
Citrus limon	Rutaceae	2
Sloanea australis	Elaeocarpaceae	1
Argyrodendron trifoliolatum	Sterculiaceae	2
Callistemon viminalis	Myrtaceae	1
Melaleuca sp.	Myrtaceae	6
Austromyrtus bidwillii	Myrtaceae	1
Acmena smithii	Myrtaceae	2

The mean height of 43 nests was 8.0 ± 6.5 m above ground level. Nest height ranged from 2 m above ground (in a garden shrub at Iluka township, RAOU Nest Record Scheme 684/1/73) to 30.5 m above ground (placed against the trunk of a Bunya Pine *Araucaria bidwillii* in the Bunya Mountains, QM O.22174).

Nest-site characteristics are summarized in Table 8.2. More than 80 % of the nest locations were well-camouflaged sites in clumps of vines or mistletoe, or in dense foliage of the nest plant itself. Clumps or tangles of vines were by far the most frequent nest location. Nests were built in prickly species of vine, such as Southern Lawyer Vine *Calamus muelleri* and Cockspur Thorn *Cudrania cochinchinensis*, as well as in non-prickly species, such as Water Vine *Cissus antarctica* and Three-leaf Water Vine *Tetrastigma nitens*. Nests were commonly situated near the top of the nest plant.

Several observations suggest that females may use the same nesting area over successive years: CHAFFER (1932) discovered an old nest in the same tree where he observed an active nest, and found another old nest nearby. CHAFFER presumed that all three nests had been built by the same individual. F.F. JAMES observed a female building a nest in the same garden shrub at Iluka township in three successive years (RAOU Nest Record

Table 8.2. Site characteristics of Regent Bowerbird nests (n = 37 nests).
Tab. 8.2. Standort-Charakteristika von Gelbnacken-Laubenvogel-Nestern (n = 37 Nester).

Nest site	Number of nests
Clump or tangle of vines	26 (70.3 %)
Clump of mistletoe	2 (5.4 %)
Dense foliage near top of nest plant	3 (8.1 %)
Forked branches or branch near trunk	3 (8.1 %)
Rather open location	3 (8.1 %)

Scheme 684/1/73). Unfortunately, it was not recorded whether this female was a banded individual; however, it seems possible that it had indeed been a banded individual, since more than 100 Regent Bowerbirds had been banded at Iluka by that time (ABBBS microfiches).

There is only one record on the spatial dispersion of nests: C.A.C. CAMERON, while observing a brooding female, found three other active nests within a 200 yard (= 183 m) radius; two of these were within a 50 yard (= 46 m) radius (QM O.22174). BERULDSEN (1980 and in litt.) stated that nests are usually well away from bowers but found one nest little more than 20 m away from a bower. The three nests found in the Sarabah Range were 120 m, 345 m and 580 m away from the nearest bower, respectively.

Eggs: clutch size, egg dimensions, proportionate egg mass, laying interval, incubation and hatching

Of 135 clutches with known clutch size, 112 (83.0 %) contained two eggs, 17 (12.6 %) contained only one egg and six clutches (4.4 %) contained three eggs. Thus, the mean clutch size of Regent Bowerbirds was 1.92 ± 0.41 eggs (for illustrations of eggs see CAMPBELL 1900; NORTH 1901-1904; LE SOUEF 1909; BERULDSEN 1980; THRELFO 1985; SINDEL 1989).

Mean linear egg dimensions were 38.26 ± 1.39 mm (n = 196) length and 26.85 ± 0.65 mm maximum breadth (n = 197). Eggs from clutches containing only one egg were, on average, longer (39.78 ± 2.51 mm, n = 12) and wider (26.92 ± 0.83 mm, n = 13) than eggs from clutches containing two or three eggs (38.17 ± 1.24 mm, n = 182, and 26.85 ± 0.64 mm, n = 182, respectively). The size difference in length was highly significant (Student's t-test, t = 4.003, *d.f.* = 192, $P < 0.0001$), whereas the difference in width was not (t = 0.384, *d.f.* = 193, $P > 0.05$).

Fresh egg mass was estimated, as it has not been weighed directly. The mean linear egg dimensions of 38.26 mm length and 26.85 mm maximum breadth resulted in a mean egg volume of 14.44 cm^3, when using $K_V = \pi : 6$; when using $K_V = 0.51$, the estimated mean egg volume was 14.07 cm^3. Assuming a specific gravity of 1.05 g/cm^3, these volume estimates resulted in estimated fresh egg masses of 15.16 g and 14.77 g, respectively.

The mean body mass of a female Regent Bowerbird was 115.8 g (see Table 3.2). Thus, the two volume estimates resulted in proportionate egg masses (expressed as the percentage of female body mass) of 13.1 % and 12.8 %, respectively.

The interval between the laying of eggs of one clutch as well as the incubation period has only been observed in captivity: SINDEL (1989) recorded egg-laying intervals of two days in three clutches of two eggs each. In each of these cases, incubation commenced with the second egg. In a clutch containing only one egg, incubation commenced one day after egg-laying. PHILLIPS (1901-1911) recorded an incubation period of 18 or 19 days, whereas BROWN (1956) observed an incubation period of 20.5 days. SINDEL (1989) recorded hatching 17 days after egg-laying, after an incubation period of only 16 days. Replacement clutches were regularly laid after nest failure (SINDEL 1989), but there is no evidence of females re-nesting in the same season after a successful breeding attempt.

Nestlings, fledglings and parental behaviour

The complete nestling period has only been observed in captivity: SINDEL (1989 and pers. comm.) recorded that seven days after hatching the eyes of a nestling commenced to open and early pin-feather development was visible on the wings; two weeks after hatching the remiges were well developed but down plumage still covered head and back. Fledging was observed 18 days after hatching, the size of the fledgling was little more than half the size of the adult. At an age of ten weeks the fledgling was comparable in size to the female. There are no quantitative data on nestling growth.

The nestling diet could be assessed at one of the nests discovered in the Sarabah Range. Colour-banded female WRO was the only adult Regent Bowerbird attending this nest. Unfortunately, the nest was only discovered at the end of the nestling period: it was discovered on 17 February 1992 at midday, and the two nestlings fledged in the afternoon of the next day. The nest location was completely covered by vines, making direct observation of the female feeding nestlings impossible. However, in 62 of 65 observed nest approaches, female WRO was first seen flying to branches or vines within a 5 m radius of the nest location, and looking around, before hopping to the nest through the foliage (in the remaining 3 nest approaches, the female could have been missed before her arrival at the nest). This behaviour made it possible to identify 36 nestling meals (see Table 8.3). This figure is smaller than the number of nest approaches observed, because the female sometimes arrived with almost completely closed mandibles and/or food items were too small to be identified. Of the 36 identified meals, 9 (25.0 %) consisted of fruit and 27 (75.0 %) of insects, indicating a predominance of insects in the nestling diet.

During 640 minutes of observation time at this nest, female WRO spent 83.2 minutes at the nest. Nest attendance was, thus, 13.0 % of observation time. Female WRO was observed spending another 109.7 minutes within a 20 m radius of the nest (= 17.1 % of observation time). The nest attendance was 13.5 % on the day before fledging (observation time 240 minutes) and 12.7 % on the fledging day (observation time 400 minutes). The

Table 8.3. Diet of Regent Bowerbird nestlings in the Sarabah Range (n = 36 identified meals of two nestlings).
Tab. 8.3. Nahrung von Gelbnacken-Laubenvogel-Nestlingen in der Sarabah-Bergkette (n = 36 identifizierte Mahlzeiten von zwei Nestlingen).

Food item(s)	Number of meals
Fruit:	
• Arils of *Diploglottis cunninghamii* (2x1 aril, 4x2 arils, 1x3 arils, 1x1 aril together with 1 yellowish drupe, possibly of *Melia azedarach*)	8 meals
• Drupes of *Elaeocarpus obovatus* (3 drupes in the 1 meal)	1 meal
Total number of fruit meals	9 meals
Insects (all meals consisted of one insect):	
• Lepidopteran caterpillars	15 meals
• Katydids (Tettigoniidae)	4 meals
• Beetles (Coleoptera)	2 meals
• Hymenoptera	2 meals
• Cockroach (Blattodea)	1 meal
• Cricket (Gryllidae)	1 meal
• Bladder Cicada *Cystosoma saundersii*	1 meal
• White butterfly (Pieridae)	1 meal
Total number of insect meals	27 meals

mean number of nest visits per hour was 6.2 ± 1.8 (n = 9 hours) and ranged from two to eight visits. The mean length of nest visits was 72 ± 51 seconds (n = 65 visits) and ranged from 25 to 345 seconds.

The two fledglings from this nest left the nest at an interval of 21 minutes. After leaving the nest, the fledglings hopped from vine to vine heading in different directions. They then sat on vines or branches within a 10 m radius of the nest location, but never together. One day after fledging, neither the fledglings nor the female could be found in the vicinity of the nest.

In the Sarabah Range, female Regent Bowerbirds were observed to feed juveniles as late as the end of April. In view of the timing of egg-laying and the duration of incubation, the juveniles were still being fed at an age of more than two months.

Nesting success and nest predators

Due to the fact that egg collections were the main source of data, there were very few data on nesting success. CHAFFER (1932 and pers. comm.) observed two nests near Gosford, one of which produced one fledgling after it had previously contained two nestlings, the other nest was deserted after the single, half-incubated egg had been robbed. An egg collected from a nest containing only one egg near Forster proved to be infertile

(SAM B22147). L. HARVEY (notebook in the Museum of Victoria) observed a nest in the Crow's Nest area near Ravensbourne producing two fledglings.

Of the three nests discovered in the Sarabah Range, one nest never contained any eggs, one nest had two nestlings which were removed by an unknown predator, and only the third nest was successful and gave rise to two fledglings (see above).

Summarizing these meagre data of seven nests, a total of ten eggs was laid in six nests, a total of eight eggs hatched in four nests and a total of five nestlings fledged from three nests. Egg success, the percentage of eggs producing fledglings, was 50.0 % (five out of ten), and nesting success, the percentage of nests producing at least one fledgling, was 42.9 % (three out of seven).

Potential predators of Regent Bowerbird nest contents include: Lace Monitor *Varanus varius*, Carpet Python, Brown Goshawk, Grey Goshawk, Green Catbird, Satin Bowerbird, Paradise Riflebird, Pied Currawong, Torresian Crow *Corvus orru*, Spotted-tailed Quoll *Dasyurus maculatus* and Feral Cat *Felis catus*. All the listed species have been observed in the Sarabah Range study area during the period of field work.

8.4 Discussion

The period of egg-laying

BERULDSEN (1980) gave the nesting season of the Regent Bowerbird as October to January. This is largely correct, although egg-laying may commence in September. NORTH (1901-1904, p. 65) claimed that "in the brushes of the northern coastal rivers of New South Wales, November and the three following months constitute the usual breeding season of this species; but near the southern limit of its range, it commences a month earlier". While there is no evidence of eggs being laid in the wild as late as February, data on the timing of the period of egg-laying of the Regent Bowerbird confirm NORTH's claim of earlier breeding in the southern part of its range.

The earlier timing of breeding attempts in southern populations (Fig. 8.1) provides support for the 'plant response model' of the environmental control of breeding (see NIX 1976). According to this model, the availability of the food of birds either directly or indirectly depends on the primary productivity of plants, which is a response to the physical environment. In areas south of the line of equal summer/winter moisture index, plant growth peaks in spring, whereas it peaks in summer in areas north of this line, as a response to the later peak in precipitation (NIX 1976, 1981). This results in earlier peaks in food availability and, ultimately, in an earlier breeding season in the southern part of the range of the Regent Bowerbird.

There are no data on the seasonal variation in the availability of insect food in different parts of the range of this species. However, peaks in monthly rainfall have been found to result in peaks of insect numbers and biomass in an Australian upland tropical rainforest (see FRITH & FRITH 1985a), and a similar pattern is likely for the subtropical rainforests within the range of the Regent Bowerbird.

Data of breeding attempts in the Big Scrub area (Fig. 8.2) suggest that the period of egg-laying of Regent Bowerbirds is slightly shorter on a local scale, i.e. in a specific locality, than over its entire distribution. However, egg-laying in separate breeding seasons in this locality still extended over a period of at least two and a half months (Fig. 8.3). Therefore, egg-laying was sufficiently asynchronous to provide multiple mating opportunities for individual male Regent Bowerbirds.

Comparison of the breeding biology and parental behaviour of bowerbird species
Breeding biology and parental behaviour of the Regent Bowerbird closely resemble other uniparental species of the bowerbird family. For the first time, uniparental female brood care in the Regent Bowerbird could be confirmed through observations of a colour-banded female individual as the only adult individual attending a nest.

The nest attendance of 13.0 % of observation time is similar to figures for other bowerbirds. Nest attendance averaged 16.4 % of observation time in Satin Bowerbirds (DONAGHEY 1981), 10.6 % in Fawn-breasted Bowerbirds (FRITH & FRITH 1989) and 12.4 % in Great Bowerbirds (FRITH & FRITH 1990a). Figures for two bowerbird species in tropical rainforests of north-eastern Queensland were higher: 35.7 % in Tooth-billed Bowerbirds (FRITH & FRITH 1985b) and 24.7 % in Golden Bowerbirds (FRITH & FRITH 1998b). The figure for the Regent Bowerbird probably underestimated the overall female time investment, as observations were only made at the end of the nestling period. DONAGHEY (1981) found that nest attendance in Satin Bowerbirds was 21.3 % of observation time in the first half of the nestling period but only 12.2 % in the second half. The latter figure is remarkably similar to the 13.0 % of the Regent Bowerbird. The percentages of nest attendance in the biparental catbirds were higher, 40.7 % in Green Catbirds (DONAGHEY 1981) and 44.4 % in Spotted Catbirds *Ailuroedus melanotis* (FRITH & FRITH 1990a).

The indirect nest approach of the female Regent Bowerbird is similar to female Tooth-billed, Golden, Satin and Great Bowerbirds, whereas the biparental Spotted Catbirds typically fly directly to the nest (FRITH & FRITH 1985b, 1998b) as is implied for the Green Catbird by DONAGHEY (1981). FRITH & FRITH (1985b) argued that this behavioural difference may reflect differences in the predatory pressure at the nest between uniparental and biparental species, as indicated by lower nesting success rates in the uniparental species.

Although the nestling diet of the Regent Bowerbird consisted mainly of insects (75.0 % of nestling meals), the predominance of insects was less marked than in the nestling diet of Satin Bowerbirds, where DONAGHEY (1981) found 95.3 % insect meals. Animal food constituted 55.8 % and 59.3 % of the nestling meals of Great and Spotted Bowerbirds, respectively (FRITH & FRITH 1990a,c), but only 35.4 % of the nestling meals in biparental Green Catbirds (DONAGHEY 1981), 29 % in uniparental Archbold's Bowerbirds (FRITH & FRITH 1994a) and 32 % in uniparental Golden Bowerbirds (FRITH & FRITH 1998b). According to these data, protein-rich animal food often, but not always, dominates in the nestling diets of uniparental bowerbird species and may be important in facilitating uniparental brood care.

However, the data on Archbold's and Golden Bowerbirds suggest that there is not always a predominance of animal food in the nestling diet of uniparental species. Therefore, differences between fruits in their nutritional value need to be considered. For example, capsular arillate fruits are often comparatively rich in proteins and lipids (CROME 1975; BEEHLER 1983a). Interestingly, eight of the nine identified fruit meals of Regent Bowerbird nestlings consisted of the capsular arillate fruit of *Diploglottis cunninghamii* (Table 8.3).

The nests of most bowerbird species are sparser and more loosely constructed than those of the biparental catbirds (see photographs in CAMPBELL 1900; NORTH 1901-1904; CHAFFER 1984; FRITH & FRITH 1985b, 1989, 1990a,c; COATES 1990). The mean height of 8.0 m of Regent Bowerbird nests was considerably lower than the 23.4 m DONAGHEY (1981) found in Satin Bowerbirds. The main data source of breeding attempts of Regent Bowerbirds were egg collections, and egg collectors may have seen and collected more accessible clutches from lower nest locations.

It has often been claimed that the nests of court-clearing or bower-building bowerbird species are typically far away from any active display sites (PECKOVER 1970; PRATT 1974; BERULDSEN 1980; VELLENGA 1980b; DIAMOND 1982b; CHAFFER 1984). However, there is little evidence to support this claim. Nests and bowers have been found at a variety of distances, sometimes only a few metres apart, and it seems more likely that males and females have overlapping home ranges (WARHAM 1962; DONAGHEY 1981; PRUETT-JONES & PRUETT-JONES 1982, 1983; FRITH 1989; FRITH & FRITH 1989, 1990a,c, 1994a, 1998b). Observations indicating that female Regent Bowerbirds may use the same nesting area over successive years are in accord with findings on other promiscuous passerines (DONAGHEY 1981; FRITH & FRITH 1990c, 1992, 1994a, 1998b). The spacing of nest sites may be an important factor influencing the spatial dispersion of display sites (DONAGHEY 1981; DAVIES 1991), but it may also be that females choose nest sites in proximity to particular males (see LILL 1974b, 1976; PRUETT-JONES & PRUETT-JONES 1983; FRITH & FRITH 1992, 1998b).

The proportionate egg mass of 12.8-13.1 % of the Regent Bowerbird is higher than figures for Green Catbird, Tooth-billed Bowerbird and Satin Bowerbird (11.6-12.6 %, 11.6-12.3 % and 10.2 %, respectively; see DONAGHEY 1981; FRITH & FRITH 1985b), but lower than in the Golden Bowerbird (13.6 %; see FRITH & FRITH 1998b). This is in line with the generally inverse correlation of proportionate fresh egg mass and female body mass (LACK 1968), as the Regent Bowerbird is larger than the Golden Bowerbird and smaller than the other three species. The proportionate egg mass of the five bowerbird species mentioned is rather high for passerines of their size. A similar phenomenon has also been found in the Neotropical cotingas (SNOW 1982), which have many similarities to bowerbirds in their evolutionary ecology.

Most species in the bowerbird family, both uniparental species and biparental, share a number of aspects in their breeding biology: they lay small clutches (1-3 eggs, most often 2 eggs), their incubation and nestling periods are similar (around 20 days), and even asynchronous egg-laying is not unique to the uniparental species (BERULDSEN 1980; DONAGHEY 1981; DONAGHEY et al. 1985; FRITH & FRITH 1985b, 1989, 1990a,c, 1998b). Archbold's Bowerbird has considerably longer incubation and nestling periods, possibly reflecting adaptation to a colder environment (FRITH & FRITH 1994a).

Small clutches, low rates of annual productivity and prolonged breeding seasons are typical of many passerines in the Australo-Papuan region (see YOM-TOV 1987; FORD 1989; COATES 1990; ROWLEY & RUSSELL 1991). According to figures from DONAGHEY (1981), FRITH & FRITH (1985b, 1994a, 1998b) and this study, the mean clutch size of bowerbird species may be slightly larger in the biparental catbirds (2.12 eggs in Green Catbirds and 2.03 in Spotted Catbirds) than in uniparental bowerbird species (1.97 eggs in Satin Bowerbirds, 1.92 in Regent Bowerbirds, 1.80 in Golden Bowerbirds, 1.50 in Tooth-billed Bowerbirds and 1.00 in Archbold's Bowerbirds). However, productivity per breeding season is low in all species in the bowerbird family. Biparental species do not appear to be capable of rearing larger broods than uniparental species, nor are they capable of rearing broods in a shorter period of time. This may have been a factor promoting male emancipation and uniparental female brood care in bowerbirds.

9 General Discussion: The Mating System of the Regent Bowerbird and the Species' Position in Bowerbird Evolution

9.1 The mating system of the Regent Bowerbird

The term 'mating system' refers to the way in which individuals of a species or a population "obtain mates, including a description of how mates are aquired (*sic*), how many mates, the characteristics of pair bonds and patterns of parental care by each sex" (DAVIES 1991, p. 263).

The mating system of the Regent Bowerbird, as described in this paper, resembles the mating systems of the other non-monogamous, bower-building species of the bowerbird family (i.e. all species of the family except catbirds *Ailuroedus* spp., see Chapter 1) in some aspects but differs in others. In the following, these similarities and differences are discussed separately.

9.1.1 Similarities to other bower-building species

The mating system of the Regent Bowerbird shows many similarities to that of the Satin Bowerbird, the most thoroughly studied bowerbird species (see Chapter 1). In both species, males build and decorate avenue bowers (section 6.3.1) which they use for their sexual displays. Though males also display to females in trees away from bowers, the most intense courtship displays are performed at bowers, and copulation always takes place at the bower or in the immediate vicinity of it (section 7.3.1). Bowers are built at dispersed sites (section 6.3.2), each bower is maintained by a single male (Table 7.1), and females visit the bowers of several males before mating (section 7.3.1). Individual males may mate with several females in a single mating season, whereas some males do not mate at all (section 7.3.1).

The duration of female visits at Regent Bowerbird bowers was found to correlate with an index of bower quality (section 7.3.1), a pattern which corresponds to female preferences for males with well-constructed bowers found in Satin Bowerbirds (BORGIA 1985a). Males of both species destroy bowers of other males and steal decoration objects from them (section 7.3.2). Males focus the majority of their bower raiding on the bowers of their nearest neighbours (Table 7.8, Fig. 7.9), their most likely sexual competitors (BORGIA 1985b). Observations of interactions of male Regent Bowerbirds (section 7.3.2) and Satin Bowerbirds (BORGIA 1985b) suggest that male dominance is important for the ability of an individual to hold a bower. As in the Satin Bowerbird (see DONAGHEY 1981), females provide uniparental brood care in the Regent Bowerbird, whereas males are emancipated (Chapter 8).

The bowers of other species may differ considerably in structure and decoration (Figs 1.1-1.2, Table 6.12), but the mating systems of all bower-building species are generally assumed to resemble the pattern described above (Borgia et al. 1985; Donaghey et al. 1985; Diamond 1986b; Pruett-Jones & Pruett-Jones 1994; Frith & Frith 1998a), although details of their mating behaviour have been studied in only some of them (e.g. Pruett-Jones & Pruett-Jones 1982, 1983; Frith 1989; Borgia & Mueller 1992; Borgia 1995a,b). The Tooth-billed Bowerbird is the only non-monogamous bowerbird species that does not build a bower (Frith & Frith 1985b, 1994b, 1995) and differs from bower-building species in having its display courts aggregated instead of dispersed (G. Borgia pers. comm.; Crome & Moore 1989; Frith & Frith 1995).

Based mainly on observations of the Satin Bowerbird, the mating systems of bowerbirds have been termed "promiscuous rather than polygamous" (Vellenga 1970, p. 10), "polygamous, males probably promiscuous" (Donaghey 1981, p. 198), 'polygynous' (Pruett-Jones & Pruett-Jones 1982; Borgia 1985b, 1986b; Borgia et al. 1985) and 'polygynous with promiscuous males and uniparental female brood care' (Frith & Frith 1985b, 1989, 1990a,c). This seemingly varied terminology is mainly attributable to differences in the authors′ classification and definitions of mating systems rather than to actual differences in their assessment of the mating systems. Numerous attempts to categorize mating systems (e.g. Selander 1972; Emlen & Oring 1977; Wittenberger 1979; Oring 1982) have created some confusion instead of a generally accepted terminology.

A main difference between classifications of mating systems is the way in which the duration of the pair bond or mate association has been considered. 'Polygamy' has been used as a collective term for all systems involving multiple mating (Emlen & Oring 1977; Oring 1982; Krebs & Davies 1987; Ford 1989; Brooke & Birkhead 1991) or, alternatively, only for those non-monogamous mating systems involving pair bond (Selander 1972; Bezzel & Prinzinger 1990). Likewise, some authors have used the term 'polygyny' to describe all mating systems where individual males control or gain access to multiple females (Emlen & Oring 1977; Oring 1982), whereas others have used 'polygyny' only where individual males mate with several females and some pair bond is developed (Selander 1972), while using 'promiscuity' where the sexes come together only for mating (Wittenberger 1979; Ford 1989; Bezzel & Prinzinger 1990; Davies 1991).

The term 'promiscuity' has been criticized because it "connotes a lack of discrimination in choice of partners" (Selander 1972, p. 193). In bowerbirds, however, there is clear evidence that females do discriminate between males (Borgia 1985a, 1995b; Borgia & Mueller 1992; this study). 'Promiscuity' also implies that there is a mixture of polygyny and polyandry, i.e. both males and females copulate several times with different individuals (Krebs & Davies 1987; Bezzel & Prinzinger 1990; Brooke & Birkhead 1991). Observations of individually marked Satin Bowerbird females, however, "indicated that multiple copulations at different bowers are rare" (Borgia & Mueller 1992, p. 12), whereas individual males were regularly observed to mate with several females in a single mating season (Borgia 1985a). This sex difference is not discernible from the term 'promiscuity'.

SELANDER (1972) proposed the term 'polybrachygyny' to describe mating systems where individual males mate with several females and a pair bond is very brief or absent. This term would correctly describe the mating systems of male Regent and Satin Bowerbirds, and probably all other bower-building species. It seems possible that SELANDER's (1972) term 'monobrachygamy' could apply to the vast majority of female bowerbirds. However, our knowledge of the mating behaviour of female bowerbirds is not as complete as our knowledge of males.

EMLEN & ORING (1977), criticized a classification of mating systems based only on the number of mates that one sex can accumulate and the duration of pair bond or mate association, without including considerations of the ecological and behavioural basis. Therefore, the term 'male-dominance polybrachygyny' may be preferable to describe the mating systems of bowerbirds. This term combines the unambiguous word 'polybrachygyny' (i.e. individual males mate with several females without a lasting bond) with the additional information that males cannot control access to females directly, nor can they control access to females indirectly by monopolizing critical resources (EMLEN & ORING 1977; ORING 1982). Instead of female defence or resource defence, the 'male-dominance polybrachygyny' of bower-building species is the consequence of female choice of particular males with the ability to build, maintain and display at well-constructed bowers (BORGIA 1985a,b, 1986a, 1995b; BORGIA et al. 1985; BORGIA & GORE 1986; BORGIA & MUELLER 1992).

As a further specification, the mating systems of the bower-building species (but not that of the court-clearing Tooth-billed Bowerbird, see above) may be classified as 'dispersed male-dominance polybrachygyny' (see ORING 1982; PRUETT-JONES & PRUETT-JONES 1982), in order to emphasize that males, and their display courts, are dispersed and not aggregated or clumped.

The factors underlying the dispersion of bowers are, however, poorly understood. In animal species where males do not provide parental care, it is generally assumed that male dispersion is primarily influenced by female dispersion, whereas female dispersion is primarily influenced by resource dispersion (DAVIES 1991), but this has not yet been tested in bowerbirds. An important factor which may have prevented bowerbird males from displaying at aggregated sites is the susceptibility of bowers to destruction (PRUETT-JONES & PRUETT-JONES 1982, 1983, 1994; COLLIAS & COLLIAS 1984).

9.1.2 Differences to other bower-building species

In spite of the general similarity between the mating system of the Regent Bowerbird and those of other bower-building species, several aspects of the mating behaviour contrast sharply with other bowerbirds. Male Regent Bowerbirds build smaller bowers, decorated with fewer objects (Tables 6.3, 6.6, 6.7 and 6.12). The bowers are maintained for a shorter period of time and their locations are changed more often (Table 7.1, Figs 7.9-7.10). Bower-owning males spend considerably less time at or near their bowers (Tables

7.3-7.4, Fig. 7.1). The initial interaction between males and females does not take place at their bowers (Table 7.6), and successful courtship displays are of a much longer duration than in other bowerbird species (section 7.3.1).

Due to the low investment in bower attendance by bower-owning males, the probability that a bower owner is present and able to defend his bower when an intruder visits it is very low (see Chapter 7). This contrasts with other species, in which bower owners actively defended their bowers from intruders much more often (PRUETT-JONES & PRUETT-JONES 1982, 1983; BORGIA 1985b, 1986a, 1995a). Instead, male Regent Bowerbirds appear to protect their bowers by building them in dense liana thickets (section 6.3.2).

It has been suggested that 'display site defence' should be included in the term for the mating systems of bowerbirds (see DAVIES 1991). This may be possible in those species in which males invest more time in bower attendance and bower defence. In the case of the Regent Bowerbird, however, the expression 'display site defence' appears to be inappropriate as this would overemphasize the incidence of direct bower defence.

The duration of female visits at Regent Bowerbird bowers was found to correlate with an index of bower quality, but it was not correlated with numbers of decoration objects (section 7.3.1). In the Satin Bowerbird, however, male mating success was found to correlate both with measures of bower quality and with numbers of decoration objects (BORGIA 1985a). These findings support BORGIA's (1985a) suggestion that, while the ultimate basis for female choice may be the same in all bower-building species, females of different bowerbird species may differ in how they assess male quality. However, as long as the ultimate basis for female choice is the same, a difference in mate assessment between females of different species does not mean that different terms for their mating systems are necessary. Therefore, the proposed term 'dispersed male-dominance polybrachygyny' may be appropriate for both the Regent Bowerbird and all other bower-building species.

9.2 The position of the Regent Bowerbird in bowerbird evolution

9.2.1 The origin of bower building and the 'transferral effect' in bowerbird evolution

If bower-building behaviour evolved as part of a mechanism allowing females to assess the quality of males as mates, as PRUETT-JONES & PRUETT-JONES (1983) and BORGIA et al. (1985) proposed in their 'marker hypothesis' (see Chapter 1), then it is possible that the small bowers of Regent Bowerbirds and the small number of decoration objects give females relatively small amounts of information about the quality of bower owners. However, the information provided by bowers and decorations could be supplemented by extended courtship displays. This view is supported by two findings (section 7.3.1): (a) in the Regent Bowerbird, the duration of female bower-visits was not correlated with numbers of decoration objects in bowers, which contrasts with the Satin Bowerbird; (b) successful courtship displays were several times longer in the Regent Bowerbird than in other bowerbird species.

These findings also support GILLIARD's (1956, 1963, 1969) hypothesis of a 'transferral effect' (see Chapter 1). According to this hypothesis, the Regent Bowerbird represents an early stage in the evolution of bower building where the bower has not yet replaced the elaborate adult male plumage (see Chapter 3) in its function as secondary sexual characteristics informative to females. Instead, in the Regent Bowerbird the display performance appears to be of particular importance for female mate choice and male mating success (see Chapter 7).

The hypothesis of a 'transferral effect' in bowerbird evolution has received further support from recent analyses of the genetic distances determined by protein electrophoresis (CHRISTIDIS & SCHODDE 1992) and from mitochondrial DNA sequences (KUSMIERSKI et al. 1993). The results of these analyses support the view that the three genera building avenue bowers (*Sericulus*, *Ptilonorhynchus* and *Chlamydera*, see section 1.2) form a monophyletic group. Mitochondrial DNA sequences (KUSMIERSKI et al. 1993) indicate a pattern of divergence among the three genera that accords with GILLIARD's hypothesis: the early divergence of the Regent Bowerbird and the later divergence of *Chlamydera* species support GILLIARD's suggestion that brightly-coloured males building small and meagrely-decorated bowers represent an ancestral condition in the evolution of bowerbirds.

GILLIARD's hypothesis of a 'transferral effect' has frequently been quoted in the literature (e.g. SCHODDE 1976; DIAMOND 1982a,b, 1986a,b; PRUETT-JONES & PRUETT-JONES 1983; COLLIAS & COLLIAS 1984; BORGIA 1985a,b, 1986a; BORGIA et al. 1985; FORD 1989; MÜLLER 1990; FRITH & FRITH 1998a). However, the hypothesis contributes little to explaining the origins of bower-building behaviour.

MARSHALL (1954, p. 171) suggested "that bower-building may have originated as a displacement activity that is fundamentally allied to nest building". DIAMOND (1982b, p. 101) also proposed that the construction of bowers "may have its origins in nest construction" and that the decoration of bowers "may have stemmed from courtship feeding". BORGIA et al. (1985), however, have rejected any functional connection between nests and bowers and stressed that bowers differ considerably from nests in their structure, terrestrial location and decoration.

The small and simple bowers of the Regent Bowerbird, which are assumed to represent an ancestral condition in the evolution of bowerbirds, do not resemble nests more than the bowers of other species. Instead, the structure of Regent Bowerbird bowers closely resembles a smaller version of Satin Bowerbird bowers (see Figs 1.2d-e and Plates 6 and 12). The main characteristic of these avenue bowers are their parallel and vertical walls which contrast with the circular placement of sticks in nests. DIAMOND (1986b), however, emphasized that the hypothesis that bowers developed from courtship nests in the past does not imply that bowers need to resemble nests today. But if the term 'nest' is used here in its broadest possible sense it could be argued that its use in this context is confusing rather than helpful.

More recently, BORGIA (1995a, p. 11) suggested that "bowers evolved to encourage female visitation at male courts by reducing the threat of forced copulation by the bower owner". The function of bowers as indicators or 'markers' of the status of males used by females in their mate choice would then appear "to be a secondary adaptation that occurred after bower-building evolved" (BORGIA l.c.).

9.2.2 Factors important in bowerbird evolution

Numerous models of sexual selection have been proposed to explain the evolution of exaggerated male display characters (for reviews see, e.g., BORGIA 1987; HARVEY & BRADBURY 1991; ANDERSSON 1994; COCKBURN 1995). Among the best known are runaway models, good genes models and handicap models. Runaway models assume that male display characters evolve as a result of a self-reinforcing coevolution of male display and female choice (FISHER 1930; LANDE 1981). Good genes models claim that females choose males that are vigorous (TRIVERS 1972; ANDERSSON 1986), older (HALLIDAY 1978), dominant (BORGIA 1979; BORGIA et al. 1985) and/or resistant to diseases (HAMILTON & ZUK 1982), because such males are more likely to lead to heritable viability gains for offspring. Handicap models suggest that exaggerated male display characters are selected if they advertise viability by handicapping the survival chances of their otherwise healthy possessors (ZAHAVI 1975, 1977).

BORGIA (1985a,b, 1986a, 1987, 1993, 1995a,b) considered how observations of male-male competition and patterns of female choice in bowerbirds conform with these sexual selection models, and concluded that both male dominance and male age may be important in sexual selection in bowerbirds. According to BORGIA et al. (1985) and BORGIA (1986a), similar selection pressures may have shaped both the evolution of bower building and decorating behaviour, and the display of showy plumage. However, a sexual selection model claiming that females prefer dominant and/or older males does not explain why evolution led to brightly-coloured males in some bowerbird species, whereas it led to elaborate display sites in others. Thus, the factors which may have caused a transfer of secondary sexual characteristics from male plumage to the display courts during the evolution of bowerbirds remain to be explained.

DIAMOND (1988, p. 647) suggested that a well-decorated bower may constitute "a much more comprehensive test of male genetic quality" than does a bright male plumage. Knowledge of the similarities and differences between the evolutionary ecology of the Regent Bowerbird and other bowerbird species makes it possible to summarize and discuss a number of other factors that may have been important in bowerbird evolution, in particular in the evolution of plumage patterns and bower structures. The following discussion is divided into separate sections corresponding to proposed early, intermediate and late evolutionary stages. The discussion is focused on the three genera building avenue bowers, because most comparable data refer to species belonging to this group.

The early stage: *Sericulus*

Molecular-biological studies of the phylogenetic relationships of bowerbirds indicate an early branching of the monogamous catbirds and suggest a monophyletic origin of all bower-building or court-clearing species (SIBLEY & AHLQUIST 1985; KUSMIERSKI et al. 1993). This accords with the general assumption of monogamy as the ancestral condition in birds (LACK 1968; ORIANS 1969; ORING 1982), but not with BOCK (1963) and GILLIARD (1969) who considered monogamy in the catbirds to be adapted secondarily.

A number of factors may have been important in the evolution of a non-monogamous mating system and bower building. A predominantly frugivorous diet may have enabled bowerbirds to satisfy their daily energy requirements in short periods of time, and made it possible for male bowerbirds to invest more time in advertising activities (see Chapter 4). Several characteristics of the breeding biology of bowerbirds may have promoted male emancipation (see Chapter 8): (a) male parental care does not appear to increase productivity rates, and (b) egg laying is sufficiently asynchronous to provide multiple mating opportunities for individual males. Low amounts of investment in single nesting attempts were made possible by the high survival rates of bowerbirds (see Chapter 5). A similar combination of ecological influences and life history features has probably been important in promoting non-monogamous mating systems in the Neotropical cotingas and manakins (see, e.g., SNOW 1962a,b, 1982; SNOW & LILL 1974; LILL 1974a,b, 1975, 1976).

DNA data indicate that the markedly sexually-dimorphic genus *Sericulus* represents an early branch in the group of species building avenue bowers (KUSMIERSKI et al. 1993). This view is supported by the simple, small and meagrely-decorated bowers of this genus (Fig. 1.2, Table 6.12) and by its relictual range (Fig. 3.1).

Several hypotheses have been proposed to explain sex- and age-related variation in plumage such as that shown by the *Sericulus* species (see BROOKE & BIRKHEAD 1991). Three hypotheses are likely to apply: (a) females (particularly when breeding), as well as immature and subadult males, may benefit from the camouflage provided by a cryptic plumage through increased likelihood of survival (cryptic hypothesis); (b) immature and subadult males may also benefit from a cryptic plumage because it signals a status different from adult males, for example, when visiting the display courts of adult males (status signalling hypothesis), and/or (c) through resembling females (female mimicry hypothesis).

The colourful plumages of adult males of the *Sericulus* species are similar to other passerines that evolved in closed forests. Their contrasting plumages can be very conspicuous during courtship displays (section 7.3.1) but nonetheless provide excellent camouflage in the canopy of closed forests (see Chapter 3).

The *Sericulus* species differ from other bowerbird species in having a reversed sexual size dimorphism, with females being larger than males (see Chapter 3). It is unknown whether this represents an ancestral condition in the evolution of the non-monogamous bowerbirds or an adaptation of males to relatively animated courtship displays in dense vegetation. It may also be that there are physiological constraints on body size in species with uniparental brood care (PAYNE 1984). At least in the Regent Bowerbird, females dominate males in aggressive encounters (Table 7.9), in accordance with the reversed sexual size dimorphism.

BORGIA (1995a, p. 11) found "the hypothesis that the bower offers protection to females from unwanted copulations by the bower owner (...) most attractive as an explanation for the origin of bower-building because it is consistent with the simplest bower type such as an undecorated sapling, all existing bower types and the behaviour of species that only clear courts". However, BORGIA did not explain how the *Sericulus* species are supposed to fit into this explanation, as their simple bowers indicate an early stage in the evolution of bower building yet their reversed sexual size dimorphism does not suggest *Sericulus* females are particularly susceptible to forced copulations by bower owners or marauding males.

The *Sericulus* species share low levels of time investment in bower attendance by bower-owning adult males (see Chapter 7). This may relate to the greater likelihood of males encountering females in the canopy. The small proportion of daytime spent at or near the terrestrial bower may also be due to a high risk of predation, as adult males are much more conspicuous when near the relatively evenly lit and plain-coloured forest floor than in the contrastingly lit and multicoloured canopy. However, a total observation time of 1516 hours spent monitoring bower activities (Table 7.1) did not reveal any evidence of predation at Regent Bowerbird bowers.

Most bowers of Regent Bowerbirds are maintained for only a few days (Table 7.1, Fig. 7.10) and bower-location changes are common (Fig. 7.9). In the small percentage of daytime male Regent Bowerbirds spend at their bowers, they cannot defend them effectively against intruders. It may thus be less profitable for males to rebuild a damaged bower than to build a new one at a new site because suitable sites may be very common in their densely-vegetated habitat (see Chapters 6 and 7).

The intermediate stage: *Ptilonorhynchus*

In several respects the Satin Bowerbird, the only species in the genus *Ptilonorhynchus*, has an intermediate position between *Sericulus* species and *Chlamydera* species. The *Sericulus* species inhabit closed forests (see Chapters 3 and 6), whereas the Satin Bowerbird lives on the edges of rainforest and in woodland (DONAGHEY 1981), and the *Chlamydera* species are found in drier and more open habitats, such as woodland, savannah and grassland (FRITH & FRITH 1989, 1990a,c). *Chlamydera* species are only slightly dimorphic or monomorphic in plumage, whereas the other two genera are markedly dimorphic, but the plumage of adult male Satin Bowerbirds consists of only one colour and is less colourful than the contrasting plumages of adult males of the *Sericulus* species (see Chapter 3).

Satin Bowerbird bowers are intermediate in size and decoration between bowers of the *Sericulus* species and *Chlamydera* species (see Fig. 1.2, Table 6.12 and Plates 6, 12 and 14-16). The level of time investment in bower attendance by bower-owning adult male

Satin Bowerbirds is intermediate between data of the genera *Sericulus* and *Chlamydera* (see Chapter 7). Likewise, rates of bower destruction and decoration stealing are intermediate in the Satin Bowerbird (Table 7.10), possibly due to intermediate interbower distances in this species (see Chapter 6).

In several bowerbird species it has been observed that the male remains hidden behind his bower in early stages of courtship displays, possibly to avoid driving females away by his display, which involves many postures also used in threat displays (WARHAM 1962; PRUETT-JONES & PRUETT-JONES 1983; COATES 1990; FRITH & FRITH 1993; BORGIA 1995a; FRITH et al. 1996). A similar pattern has been observed in displays of Jackson's Widowbird *Euplectes jacksoni*, a species of weaver (Ploceidae) from highland grassland in East Africa (see ANDERSSON 1991). Males construct individual display courts through beating down a ring in the grass around a central tuft. During a courtship display a male Jackson's Widowbird adjusts his position to keep the central tuft between him and the female.

COLLIAS & COLLIAS (1984) suggested that a screening function may have been important in the evolution of bower building. This suggestion bears a resemble to BORGIA's (1995a) hypothesis that the bower offers protection to females from unwanted copulations. While a screening function does not appear to be necessary in the genus *Sericulus* with its reversed sexual size dimorphism (see above), it is possibly important in bowerbird genera in which the male is the larger sex, such as *Ptilonorhynchus* and *Chlamydera*.

The late stage: *Chlamydera*

According to SIBLEY & AHLQUIST (1985), the *Ptilonorhynchus* and *Chlamydera* lineages diverged from one another during the middle to late Miocene, about 12 million years ago, a period when the Australian continent was drying out and the rainforests were retreating (ARCHER et al. 1991). The species in the genus *Chlamydera* are the only bowerbirds inhabiting dry and open habitats (FRITH & FRITH 1989, 1990a,c). The plumages of the *Chlamydera* species are dull brown or grey (COOPER & FORSHAW 1977; EVERETT 1978).

The *Chlamydera* species build the largest bowers of the avenue type, consisting of the largest number of sticks and decorated with the largest number of objects (see Fig. 1.2, Table 6.12 and Plates 14-16). HARPER (1991) suggested that the risks of predation may have favoured a transfer of conspicuous signals from intrinsic signals, the plumages of males, to extrinsic signals: their bowers. According to PARTRIDGE & ENDLER (1987, p. 267), "the identity of traits affected by sexual selection is likely to be determined partially by sources of mortality". The plumages of adult males of the *Sericulus* species, well camouflaged in the canopy of closed forests, would certainly be extremely conspicuous in more open habitats. In contrast, the brown or grey plumages of the *Chlamydera* species conform with GLOGER's rule which states that members of a taxon tend to be paler in the drier parts of their range (FORD 1989).

Nearest-neighbour distances of *Chlamydera* bowers are larger than in all other bowerbird genera (see Chapter 6). In Spotted and Great Bowerbirds, the only *Chlamydera* species in which patterns of male-male competiton have been studied (BORGIA & MUELLER 1992; BORGIA 1995a,b), the rates of bower destruction and decoration stealing were found to be comparatively low (Table 7.10). According to BORGIA & MUELLER (1992, p. 17), "the relative rareness of bower destructions suggests that effort directed at bower-building translates into cumulative improvements in bower quality". In contrast, Satin Bowerbird males spend considerable time rebuilding their destroyed or damaged bowers (DONAGHEY 1981; BORGIA 1985b, 1986a), and Regent Bowerbird males often change bower locations and build new bowers (section 7.3.2).

When comparing the congeneric Spotted and Great Bowerbirds, BORGIA (1995a) found that male displays of Spotted Bowerbirds are extremely vigorous. BORGIA (l.c., p. 1) suggested that "increased separation between bowers has caused selection for vigorous male display as part of mate assessment".

Judged by data for the Great Bowerbird (VESELOVSKÝ 1978, 1979), the level of time investment in bower attendance by bower-owning adult males is higher in *Chlamydera* species than in the other two genera building avenue bowers. Therefore, low rates of bower raiding in the genus *Chlamydera* could also be connected with greater bower attentiveness of bower owners. Greater bower attentiveness and, possibly, stronger fidelity to bower sites in *Chlamydera* species could, in turn, be related to their more open habitats where sites suitable for bowers may be much rarer than, for example, in the closed forests inhabited by the Regent Bowerbird and its congeners.

Conclusion

This study on the evolutionary ecology of the Regent Bowerbird made it possible to compare the species with other bowerbirds, and to discuss factors that may have been important in the evolution of the family, in particular in the group of species building avenue bowers.

All non-monogamous species in the bowerbird family have many similarities in their behavioural and reproductive biology. Several aspects of their life history are nearly identical, such as a predominantly frugivorous diet in adults, high survival rates, male emancipation and uniparental female brood care. The general patterns of female mate-choice decisions and male-male competition are also similar and appear to be shaped by the same forces of sexual selection.

The marked differences among bower-building species in the elaborateness of male plumages and their respective bowers, however, appear to be influenced strongly by habitat differences and associated differences in plumage conspicuousness and predation, population density and bower-site availability. In the group of species building avenue bowers, these differences led to elaborate adult male plumages and simple bowers in the Regent Bowerbird and the other *Sericulus* species and to dull adult male plumages and elaborate bowers in the genus *Chlamydera*, with the monotypic Satin Bowerbird having an intermediate position. Therefore, even when discussing the evolution of a group of species with traits frequently quoted as typical examples of sexual selection, the pressures of natural selection should not be ignored.

Appendices

Appendix 1: Vascular plant species of the study area

The following list of vascular plant species of the study area was compiled after own data and data from McDONALD & WHITEMAN (1979). Species are arranged in alphabetical order, the nomenclature follows ANDREWS (1990) for ferns, STANLEY & ROSS (1983, 1986, 1989) for gymnosperms and angiosperms except orchids, and JONES (1988) for orchids. Information on life form and abundance rating accompany each plant name, similar to McDONALD & THOMAS (1989). Introduced species are indicated with an asterisk (*).

The following terminology of life forms was used (arranged in alphabetical order, definitions from STANLEY & ROSS 1983; LINCOLN & BOXSHALL 1987):

- Epiphyte, a plant growing on another plant for support or anchorage rather than for water supply or nutrients, i.e. non-parasitic.
- Fern, a vascular plant which reproduces by spores produced in sporangia borne on the leaves.
- Forb, a broad-leaved herbaceous plant.
- Graminoid, a narrow-leaved herbaceous plant.
- Hemiepiphyte (strangler), a plant that spends only part of its life cycle as an epiphyte, producing both aerial and subterranean roots at different times.
- Liana (liane, vine), a woody, free-hanging, climbing plant.
- Parasite, an organism intimately associated with and obtaining nourishment from another organism at the other's expense.
- Shrub, a woody plant with many stems.
- Tree, a woody plant usually with an evident trunk.

Plant species	Life form	Abundance rating
Acacia aulacocarpa	Tree	Occasional
Acacia maidenii	Tree	Occasional
Acacia melanoxylon	Tree	Occasional
Acronychia oblongifolia	Tree	Occasional
Acronychia pauciflora	Tree	Common
Actephila lindleyi	Shrub/tree	Abundant
Adiantum aethiopicum	Fern	Occasional
Adiantum formosum	Fern	Rare
Adiantum hispidulum	Fern	Occasional
Alchornea ilicifolia	Shrub	Abundant
Alocasia macrorrhizos	Forb/shrub	Occasional

Plant species	Life form	Abundance rating
Alphitonia excelsa var. *excelsa*	Tree	Common
Alyxia magnifolia	Shrub	Rare
Alyxia ruscifolia	Shrub	Occasional
Amylotheca dictyophleba	Parasite	Occasional
*Anagallis arvensis**	Forb	Occasional
Aphananthe philippinensis	Tree	Occasional
Araucaria cunninghamii	Tree	Abundant
*Araujia hortorum**	Liana	Occasional
Argyrodendron trifoliolatum	Tree	Occasional
Arytera divaricata	Tree	Occasional
Asplenium australasicum	Epiphyte/fern	Common
Austromyrtus bidwillii	Tree/shrub	Occasional
Austromyrtus hillii	Tree/shrub	Occasional
Baloghia lucida	Tree	Occasional
Bauerella simplicifolia	Tree	Rare
Brachychiton acerifolius	Tree	Occasional
Brachychiton discolor	Tree	Common
Breynia oblongifolia	Shrub	Occasional
Caesalpinia subtropica	Liana	Common
Calanthe triplicata	Forb	Rare
Callistemon viminalis	Shrub/tree	Rare
Canthium odoratum	Shrub/tree	Rare
Capparis arborea	Tree/shrub	Common
Carissa ovata var. *ovata*	Shrub	Occasional
Casearia multinervosa	Shrub/tree	Rare
Cassine australis var. *australis*	Tree/shrub	Occasional
Celastrus subspicata	Liana/shrub	Occasional
Centaurium spicatum	Forb	Rare
Cissus antarctica	Liana	Abundant
Citriobatus lancifolius	Tree/shrub	Rare
Citriobatus pauciflorus	Shrub	Occasional
Claoxylon australe	Tree	Occasional
Cleistanthus cunninghamii	Shrub/tree	Occasional
Clerodendrum floribundum	Shrub/tree	Rare
Clerodendrum tomentosum	Shrub/tree	Rare
Cordyline petiolaris	Shrub	Common
Cordyline rubra	Shrub	Rare
Croton insularis	Tree/shrub	Occasional
Croton stigmatosus	Tree	Occasional
Croton verreauxii	Shrub/tree	Occasional

Plant species	Life form	Abundance rating
Cryptocarya bidwillii	Tree	Rare
Cryptocarya triplinervis	Tree	Occasional
Cudrania cochinchinensis	Liana/shrub	Common
Cupaniopsis parvifolia	Tree	Occasional
Cyperus tetraphyllus	Graminoid	Common
Daphnandra micrantha	Tree	Rare
Deeringia amaranthoides	Forb/shrub	Occasional
Dendrobium tarberi	Epiphyte	Occasional
Dendrobium teretifolium	Epiphyte	Rare
Dendrocnide excelsa	Tree	Abundant
Dendrocnide photinophylla	Tree	Common
Denhamia celastroides	Tree/shrub	Occasional
Denhamia pittosporoides	Tree/shrub	Occasional
Derris involuta	Liana	Occasional
Dianella caerulea var. *assera*	Graminoid	Occasional
Dioscorea transversa	Liana/forb	Common
Diospyros australis	Tree/shrub	Occasional
Diospyros pentamera	Tree	Occasional
Diplocyclos palmatus	Forb/liana	Occasional
Diploglottis cunninghamii	Tree	Rare
Doodia aspera	Fern	Occasional
Drypetes australasica	Tree	Occasional
Ehretia acuminata	Tree	Occasional
Elaeocarpus obovatus	Tree	Occasional
Elattostachys xylocarpa	Tree	Common
Embelia australiana	Liana/shrub	Occasional
Erythrina vespertilio	Tree	Rare
Eucalyptus microcorys	Tree	Occasional
*Eupatorium adenophorum**	Forb/shrub	Occasional
Euroschinus falcata	Tree	Rare
Eustrephus latifolius	Liana	Occasional
Excoecaria dallachyana	Tree	Common
Ficus macrophylla	Tree/hemiepiphyte	Occasional
Ficus obliqua	Tree/hemiepiphyte	Occasional
Ficus platypoda	Tree	Rare
Ficus superba var. *henneana*	Tree/hemiepiphyte	Occasional
Ficus watkinsiana	Tree/hemiepiphyte	Rare
Flindersia australis	Tree	Occasional
Geijera salicifolia var. *latifolia*	Tree	Occasional
Geitonoplesium cymosum	Liana	Occasional

Plant species	Life form	Abundance rating
Geranium solanderi	Forb	Occasional
*Gomphocarpus physocarpus**	Shrub	Occasional
Grevillea robusta	Tree	Common
Guilfoylia monostylis	Tree	Rare
Hodgkinsonia ovatiflora	Tree	Common
Jasminum dallachii	Liana/shrub	Occasional
Jasminum simplicifolium subsp. *australiense*	Liana/shrub	Common
*Lantana camara**	Shrub	Common
Lastreopsis acuminata	Fern	Occasional
Legnephora moorei	Liana	Occasional
Lophostemon confertus	Tree	Occasional
Malaisia scandens	Liana/shrub	Occasional
Mallotus philippensis	Tree	Occasional
Maytenus bilocularis	Tree/shrub	Occasional
Melia azedarach var. *australasica*	Tree	Common
Melicope erythrococca	Tree	Rare
Microcitrus australasica var. *australasica*	Shrub/tree	Occasional
Mischocarpus anodontus	Tree	Occasional
Notelaea longifolia forma *glabra*	Shrub/tree	Rare
Nyssanthes diffusa	Forb	Common
Olea paniculata	Tree	Abundant
Oxalis corniculata var. *corniculata*	Forb	Occasional
Pandorea jasminoides	Liana	Occasional
Parsonsia straminea	Liana	Rare
Parsonsia velutina	Liana	Occasional
*Passiflora subpeltata**	Liana	Occasional
Pellaea falcata var. *nana*	Fern	Common
Pentaceras australe	Tree	Occasional
Peperomia leptostachya	Forb	Occasional
Peperomia tetraphylla	Epiphyte/forb	Rare
*Phytolacca octandra**	Forb/shrub	Occasional
Pittosporum undulatum	Tree/shrub	Abundant
Planchonella australis	Tree	Occasional
Planchonella myrsinoides	Tree/shrub	Common
Platycerium bifurcatum	Epiphyte/fern	Occasional
Platycerium superbum	Epiphyte/fern	Occasional
Plectranthus argentatus	Forb/shrub	Common
Pollia crispata	Forb	Occasional
Polyscias elegans	Tree	Occasional

Plant species	Life form	Abundance rating
Premna lignum-vitae	Tree	Common
Pseuderanthemum variabile	Forb	Common
Pseudoweinmannia lachnocarpa	Tree	Common
Psychotria daphnoides	Shrub	Common
Randia chartacea	Shrub/tree	Occasional
Rapanea variabilis	Tree/shrub	Rare
Rauwenhoffia leichhardtii	Liana	Occasional
Rhinerrhiza divitiflora	Epiphyte	Rare
Rhodamnia argentea	Tree	Rare
Rhodosphaera rhodanthema	Tree	Abundant
Rhysotoechia bifoliolata	Tree	Rare
Rubus moluccanus	Shrub/liana	Occasional
Rubus rosifolius	Shrub/liana	Occasional
Scolopia braunii	Tree/shrub	Occasional
Sicyos australis	Liana	Common
Smilax australis	Liana	Occasional
Solanum corifolium	Shrub	Common
*Solanum mauritianum**	Shrub	Occasional
Stenocarpus sinuatus	Tree	Rare
Streblus pendulinus	Tree/shrub	Abundant
Strychnos axillaris	Tree	Occasional
*Tagetes minuta**	Forb	Occasional
Tetrastigma nitens	Liana	Common
Toona australis	Tree	Rare
*Tradescantia albiflora**	Forb	Occasional
Urtica incisa	Forb	Occasional
Viola hederacea	Forb	Occasional

Appendix 2: Bird assemblage of the study area

The following list of bird species of the study area was compiled after own observations from 1989 until 1992. Species are arranged in groups, depending on feeding behaviour (definitions from Lincoln & Boxshall 1987; Kikkawa 1988; Ford 1989), habitat preferences and regularity of observations. The sequence of species within each category of feeding behaviour depends on size (total length; data from Slater et al. 1989), foraging stratum and foraging substrate. The taxonomy follows Christidis & Boles (1994), German names generally follow Wolters (1975-1982) and Perrins (1992).

During the three field seasons of this study, 99 bird species were observed; 43.6 % of the 227 species listed by Nielsen (1991) for Lamington National Park and environs, an area which includes many other types of habitat. The rare and endangered southern subspecies of the Double-eyed Fig-Parrot *Cyclopsitta diophthalma coxeni* has been observed in the study area several times during the 1970s and 1980s (Holmes 1990), but not during the field work period.

Frugivores (species predominantly feeding on fruit)

Foraging stratum: canopy
Double-eyed Fig-Parrot (Rotwangen-Zwergpapagei) *Cyclopsitta diophthalma coxeni* 13-15 cm
Rose-crowned Fruit-Dove (Königsfruchttaube) *Ptilinopus regina* 18-24 cm
Wompoo Fruit-Dove (Purpurbrust-Fruchttaube) *Ptilinopus magnificus* 35-40 cm
Topknot Pigeon (Haubenfruchttaube) *Lopholaimus antarcticus* 40-46 cm

Foraging stratum: various strata
Mistletoebird (Rotsteiß-Mistelfresser) *Dicaeum hirundinaceum* 10-11 cm
Regent Bowerbird (Gelbnacken-Laubenvogel) *Sericulus chrysocephalus* 24-28 cm
Satin Bowerbird (Seidenlaubenvogel) *Ptilonorhynchus violaceus* 27-30 cm
Green Catbird (Grünkatzenvogel) *Ailuroedus crassirostris* 29-32 cm
White-headed Pigeon (Weißbrusttaube) *Columba leucomela* 38-42 cm
Brown Cuckoo-Dove (Kuckucks- bzw. Maronentaube) *Macropygia amboinensis phasianella* 38-43 cm

Foraging stratum: ground
Wonga Pigeon (Wongataube) *Leucosarcia melanoleuca* 36-38 cm

Granivores (species predominantly feeding on seeds)

Red-browed Finch (Dornastrild) *Neochmia temporalis* 11-12 cm
Emerald Dove (Glanzkäfertaube) *Chalcophaps indica* 23-28 cm
Crimson Rosella (Pennantsittich) *Platycercus elegans* 32-36 cm
Australian King-Parrot (Königssittich) *Alisterus scapularis* 43 cm
Sulphur-crested Cockatoo (Gelbhaubenkakadu) *Cacatua galerita* 49 cm

Yellow-tailed Black-Cockatoo (Ruß- bzw. Gelbohrkakadu) *Calyptorhynchus f. funereus* 60-69 cm

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Insectivores (species predominantly feeding on insects and other arthropods)

Foraging substrate: air above rainforest canopy

White-throated Needletail (Stachelschwanzsegler) *Hirundapus caudacutus* 20 cm

Foraging substrate: air at canopy level

Rose Robin (Rosenschnäpper) *Petroica rosea* 11 cm
Spangled Drongo (Glanzfleckdrongo) *Dicrurus bracteatus* 28-32 cm

Foraging substrate: air below canopy level

White-eared Monarch (Weißohrmonarch) *Monarcha leucotis* 13 cm
Grey Fantail (Graufächerschwanz) *Rhipidura fuliginosa* 16 cm
Rufous Fantail (Fuchs- bzw. Rotstirn-Fächerschwanz) *Rhipidura r. rufifrons* 16 cm
Black-faced Monarch (Maskenmonarch) *Monarcha melanopsis* 15-20 cm

Foraging substrate: leaves

Brown Gerygone (Grauwangengerygone) *Gerygone mouki* 10 cm
Brown Thornbill (Rotstirn-Dornschnabel) *Acanthiza pusilla* 10 cm
Silvereye (Mantelbrillenvogel) *Zosterops lateralis* 12 cm
Spectacled Monarch (Brillenmonarch) *Monarcha trivirgatus* 14-16 cm
Golden Whistler (Gelbbauch-Dickkopf) *Pachycephala pectoralis* 17 cm
Shining Bronze-Cuckoo (Bronzekuckuck) *Chrysococcyx lucidus* 17-18 cm
Varied Triller (Weißbrauenlalage) *Lalage leucomela* 18-21 cm
Lewin's Honeyeater (Goldohr-Honigfresser) *Meliphaga lewinii* 19-21 cm
Brush Cuckoo (Buschkuckuck) *Cacomantis variolosus* 24 cm
Cicadabird (Mönchsraupenfänger) *Coracina tenuirostris* 24-26 cm
Fan-tailed Cuckoo (Fächerschwanzkuckuck) *Cacomantis flabelliformis* 24-28 cm
Black-faced Cuckoo-shrike (Schwarzgesicht-Raupenfänger) *Coracina novaehollandiae* 33 cm

Foraging substrate: bark

Large-billed Scrubwren (Fahlstirnsericornis) *Sericornis magnirostris* 12-13 cm
White-throated Treecreeper (Weißkehl-Baumrutscher) *Cormobates leucophaeus* 13-15 cm
Crested Shrike-tit (Meisendickkopf) *Falcunculus frontatus* 16-19 cm
Little Shrike-thrush (Waldgudilang) *Colluricincla megarhyncha* 17-19 cm
Paradise Riflebird (Schildparadiesvogel) *Ptiloris paradiseus* 28-30 cm

Foraging substrate: ground

White-browed Scrubwren (Weißbrauensericornis) *Sericornis frontalis* 11-14 cm
Pale-yellow Robin (Fahlgesichtschnäpper) *Tregellasia capito* 12-14 cm
Yellow-throated Scrubwren (Gelbkehlsericornis) *Sericornis citreogularis* 13-15 cm
Eastern Yellow Robin (Goldbauchschnäpper) *Eopsaltria australis* 15 cm

Logrunner (Stachelschwanzflöter) *Orthonyx temminckii* 17-20 cm
Noisy Pitta (Lärmpitta) *Pitta versicolor* 17-20 cm
Grey Shrike-thrush (Graubrustgudilang) *Colluricincla harmonica* 22.5 cm
Russet-tailed Thrush (Papuaerddrossel) *Zoothera heinei* 25-29 cm
Eastern Whipbird (Schwarzschopf-Wippflöter) *Psophodes olivaceus* 25-30 cm
Albert's Lyrebird (Braunrücken-Leierschwanz) *Menura alberti* 65-90 cm

Nectarivores (species predominantly feeding on nectar)
Scarlet Honeyeater (Scharlachhonigfresser) *Myzomela sanguinolenta* 10-11 cm
Eastern Spinebill (Rotnacken-Honigfresser) *Acanthorhynchus tenuirostris* 13-16 cm
Scaly-breasted Lorikeet (Schuppenlori) *Trichoglossus chlorolepidotus* 23 cm
Rainbow Lorikeet (Allfarblori) *Trichoglossus haematodus* 25-30 cm

Omnivores (species feeding on a mixed diet of plant and animal material)
Pied Currawong (Weißbürzel-Würgerkrähe) *Strepera graculina* 41-51 cm
Torresian Crow (Salvadorikrähe) *Corvus orru* 50 cm
Australian Brush-turkey (Buschhuhn) *Alectura lathami* 70 cm

Raptors (species feeding on vertebrates and other larger prey)
Southern Boobook (Kuckuckskauz) *Ninox novaeseelandiae* 30-35 cm
Peregrine Falcon (Wanderfalke) *Falco peregrinus* 38-48 cm
Grey Goshawk (Grauhabicht) *Accipiter novaehollandiae* 35-54 cm
Brown Goshawk (Bänderhabicht) *Accipiter fasciatus* 42-50 cm
Wedge-tailed Eagle (Keilschwanzadler) *Aquila audax* 90-100 cm

Common visitors in clearings, usually not in rainforest (in taxonomic order)
Masked Lapwing (Maskenkiebitz) *Vanellus miles*
Tawny Frogmouth (Eulenschwalm) *Podargus strigoides*
Laughing Kookaburra (Jägerliest) *Dacelo novaeguineae*
Rainbow Bee-eater (Regenbogenspint) *Merops ornatus*
Dollarbird (Dollarvogel) *Eurystomus orientalis*
Superb Fairy-wren (Prachtstaffelschwanz) *Malurus cyaneus*
Noisy Miner (Weißstirn-Schwatzvogel) *Manorina melanocephala*
Willie Wagtail (Gartenfächerschwanz) *Rhipidura leucophrys*
Grey Butcherbird (Graurücken-Würgatzel) *Cracticus torquatus*
Pied Butcherbird (Schwarzkehl-Würgatzel) *Cracticus nigrogularis*
Australian Magpie (Flötenvogel) *Gymnorhina tibicen*
Richard's Pipit (Australspornpieper) *Anthus novaeseelandiae*
Welcome Swallow (Neuhollandschwalbe) *Hirundo neoxena*

Uncommon visitors and vagrants (in taxonomic order)
Little Black Cormorant (Schwarzscharbe) *Phalacrocorax sulcirostris*
White-necked Heron (Weißhalsreiher) *Ardea pacifica*
Straw-necked Ibis (Stachelibis) *Threskiornis spinicollis*
Black-shouldered Kite (Australischer Gleitaar) *Elanus axillaris*
Whistling Kite (Keilschwanzweih) *Haliastur sphenurus*
Collared Sparrowhawk (Sydneysperber) *Accipiter cirrhocephalus*
Painted Button-quail (Buntlaufhühnchen) *Turnix varia*
Common Bronzewing (Bronzeflügeltaube) *Phaps chalcoptera*
Superb Fruit-Dove (Prachtfruchttaube) *Ptilinopus superbus*
Pale-headed Rosella (Blasskopfrosella) *Platycercus adscitus*
Common Koel (Koël) *Eudynamys scolopacea*
Channel-billed Cuckoo (Fratzenkuckuck) *Scythrops novaehollandiae*
Pheasant Coucal (Fasankuckuck) *Centropus phasianinus*
Spotted Pardalote (Fleckenpanthervogel) *Pardalotus punctatus*
Striated Thornbill (Stricheldornschnabel) *Acanthiza lineata*
Noisy Friarbird (Lärmlederkopf) *Philemon corniculatus*
Bell Miner (Glockenhonigfresser) *Manorina melanophrys*
Yellow-faced Honeyeater (Dreistreifen-Honigfresser) *Lichenostomus chrysops*
Brown Honeyeater (Braunhonigfresser) *Lichmera indistincta*
Jacky Winter (Weißschwanzschnäpper) *Microeca fascinans*
Leaden Flycatcher (Silbermyiagra) *Myiagra rubecula*
Satin Flycatcher (Seidenmyiagra) *Myiagra cyanoleuca*
Olive-backed Oriole (Streifenpirol) *Oriolus sagittatus*
Figbird (Feigenpirol) *Sphecotheres viridis*

Appendix 3: Colour band combinations and banding details

The following list of colour band combinations includes all 216 individual combinations possible when marking with three colour bands (in addition to the numbered metal band) and six different colours and gives details about all 203 Regent Bowerbirds (101 males and 102 females) individually marked in the Sarabah Range during the field study period from 1989 until 1992. The abbreviations used are explained below.

Colours:
B = dark blue
G = light green
N = black
O = orange
R = red
W = white

Combinations:
1st letter = colour band over metal band on right tarsus
2nd letter = upper colour band on left tarsus
3rd letter = lower colour band on left tarsus

Age code when banded (following LOWE 1989):
1+ = a bird within its first year of life or older
2+ = a bird within its second year of life or older
3+ = a bird within its third year of life or older
etc.

Colour band combination		Band number	Banding date	Sex	Age code (when banded)
1.	RRR	061-20078	01 Oct. 1989	Male	7+
2.	RRN	061-20051	17 Sep. 1989	Female	2+
3.	RRB	061-20068	24 Sep. 1989	Female	2+
4.	RRG	061-20060	19 Sep. 1989	Male	3+
5.	RRO	061-35151	16 Nov. 1989	Female	1+
6.	RRW	061-20082	03 Oct. 1989	Male	7+
7.	RNR	061-20069	24 Sep. 1989	Male	7+
8.	RNN	061-20061	19 Sep. 1989	Male	7+
9.	RNB	061-20056	19 Sep. 1989	Female	2+
10.	RNG	061-20059	19 Sep. 1989	Female	2+
11.	RNO	061-20091	16 Oct. 1989	Female	1+
12.	RNW	061-20081	02 Oct. 1989	Male	3+
13.	RBR	061-20067	24 Sep. 1989	Male	7+

Colour band combination		Band number	Banding date	Sex	Age code (when banded)
14.	RBN	061-20053	18 Sep. 1989	Male	7+
15.	RBB	061-20064	23 Sep. 1989	Female	2+
16.	RBG	061-20054	18 Sep. 1989	Female	2+
17.	RBO	061-20086	09 Oct. 1989	Female	2+
18.	RBW	061-20080	02 Oct. 1989	Male	7+
19.	RGR	061-20066	24 Sep. 1989	Male	7+
20.	RGN	061-20063	23 Sep. 1989	Male	7+
21.	RGB	061-20062	19 Sep. 1989	Female	2+
22.	RGG	061-20058	19 Sep. 1989	Male	4+
23.	RGO	061-20085	04 Oct. 1989	Female	2+
24.	RGW	061-20072	28 Sep. 1989	Male	6+
25.	ROR	061-20070	28 Sep. 1989	Female	2+
26.	RON	061-20073	28 Sep. 1989	Female	3+
27.	ROB	061-20074	28 Sep. 1989	Female	3+
28.	ROG	061-20075	28 Sep. 1989	Female	1+
29.	ROO	061-20076	01 Oct. 1989	Female	2+
30.	ROW	061-20077	01 Oct. 1989	Female	2+
31.	RWR	061-20065	23 Sep. 1989	Male	6+
32.	RWN	061-20055	18 Sep. 1989	Male	7+
33.	RWB	061-20052	17 Sep. 1989	Female	2+
34.	RWG	061-20057	19 Sep. 1989	Male	4+
35.	RWO	061-20079	02 Oct. 1989	Female	3+
36.	RWW	061-20071	28 Sep. 1989	Male	6+
37.	NRR	061-35149	12 Nov. 1989	Male	1+
38.	NRN	061-20092	16 Oct. 1989	Male	4+
39.	NRB	061-20097	01 Nov. 1989	Male	5+
40.	NRG	061-35145	08 Nov. 1989	Male	1+
41.	NRO	061-35148	11 Nov. 1989	Female	1+
42.	NRW	061-35161	25 Nov. 1989	Female	1+
43.	NNR	061-35153	18 Nov. 1989	Male	3+
44.	NNN	061-20093	16 Oct. 1989	Female	1+
45.	NNB	061-20083	03 Oct. 1989	Male	7+
46.	NNG	061-20089	13 Oct. 1989	Male	4+
47.	NNO	061-35152	17 Nov. 1989	Female	1+
48.	NNW	061-35162	04 Dec. 1989	Female	1+
49.	NBR	061-35154	19 Nov. 1989	Male	2+
50.	NBN	061-20099	05 Nov. 1989	Male	2+
51.	NBB	061-20084	04 Oct. 1989	Male	6+
52.	NBG	061-20090	14 Oct. 1989	Male	4+
53.	NBO	061-35156	21 Nov. 1989	Female	2+
54.	NBW	061-35163	15 Dec. 1989	Male	4+
55.	NGR	061-35155	20 Nov. 1989	Male	2+
56.	NGN	061-20100	05 Nov. 1989	Male	3+

Colour band combination		Band number	Banding date	Sex	Age code (when banded)
57.	NGB	061-20087	10 Oct. 1989	Male	4+
58.	NGG	061-20095	25 Oct. 1989	Male	7+
59.	NGO	061-35157	23 Nov. 1989	Female	1+
60.	NGW	061-55061	16 Dec. 1989	Male	3+
61.	NOR	061-35147	11 Nov. 1989	Female	1+
62.	NON	061-35146	08 Nov. 1989	Female	2+
63.	NOB	061-20094	17 Oct. 1989	Female	2+
64.	NOG	061-20098	01 Nov. 1989	Female	1+
65.	NOO	061-35150	15 Nov. 1989	Female	1+
66.	NOW	061-35159	23 Nov. 1989	Female	2+
67.	NWR	061-35160	24 Nov. 1989	Female	2+
68.	NWN	061-35144	05 Nov. 1989	Male	2+
69.	NWB	061-20088	13 Oct. 1989	Male	3+
70.	NWG	061-20096	27 Oct. 1989	Male	7+
71.	NWO	061-35158	23 Nov. 1989	Female	1+
72.	NWW	061-55062	20 Dec. 1989	Male	2+
73.	BRR	062-02106	22 Nov. 1990	Male	2+
74.	BRN	062-02141	19 Oct. 1991	Male	4+
75.	BRB	062-02107	25 Nov. 1990	Male	3+
76.	BRG	062-02108	29 Nov. 1990	Male	2+
77.	BRO	062-02112	31 Aug. 1991	Female	2+
78.	BRW	062-02111	18 Dec. 1990	Female	1+
79.	BNR	062-02143	19 Oct. 1991	Male	7+
80.	BNN	062-02144	21 Oct. 1991	Male	3+
81.	BNB	062-02145	23 Oct. 1991	Male	2+
82.	BNG	062-02147	24 Oct. 1991	Male	3+
83.	BNO	062-02140	15 Oct. 1991	Female	2+
84.	BNW	062-02148	01 Nov. 1991	Male	3+
85.	BBR	062-02113	01 Sep. 1991	Male	7+
86.	BBN	062-02149	01 Nov. 1991	Male	7+
87.	BBB	062-02118	25 Sep. 1991	Male	7+
88.	BBG	062-02128	06 Oct. 1991	Male	3+
89.	BBO	062-02119	26 Sep. 1991	Female	1+
90.	BBW	062-02129	06 Oct. 1991	Male	7+
91.	BGR	062-02131	07 Oct. 1991	Male	4+
92.	BGN	062-02150	04 Nov. 1991	Male	4+
93.	BGB	062-02134	08 Oct. 1991	Male	7+
94.	BGG	062-02136	08 Oct. 1991	Female	2+
95.	BGO	062-02120	28 Sep. 1991	Female	2+
96.	BGW	062-02135	08 Oct. 1991	Male	2+
97.	BOR	062-02121	28 Sep. 1991	Female	2+
98.	BON	062-02142	19 Oct. 1991	Female	2+
99.	BOB	062-02122	29 Sep. 1991	Female	2+

Colour band combination		Band number	Banding date	Sex	Age code (when banded)
100.	BOG	062-02123	29 Sep. 1991	Female	2+
101.	BOO	062-02124	04 Oct. 1991	Female	2+
102.	BOW	062-02125	04 Oct. 1991	Female	1+
103.	BWR	062-02133	08 Oct. 1991	Female	2+
104.	BWN	062-02251	05 Nov. 1991	Female	3+
105.	BWB	062-02132	07 Oct. 1991	Female	2+
106.	BWG	062-02130	07 Oct. 1991	Female	2+
107.	BWO	062-02126	05 Oct. 1991	Female	2+
108.	BWW	062-02127	06 Oct. 1991	Female	2+
109.	GRR	061-95453	22 Sep. 1990	Male	3+
110.	GRN	061-95454	22 Sep. 1990	Male	6+
111.	GRB	061-95455	22 Sep. 1990	Male	4+
112.	GRG	061-95456	22 Sep. 1990	Male	1+
113.	GRO	061-95463	03 Oct. 1990	Female	2+
114.	GRW	061-95461	02 Oct. 1990	Male	1+
115.	GNR	061-95462	02 Oct. 1990	Male	3+
116.	GNN	061-95466	03 Oct. 1990	Male	3+
117.	GNB	061-95467	04 Oct. 1990	Male	2+
118.	GNG	061-95468	04 Oct. 1990	Male	1+
119.	GNO	061-95469	06 Oct. 1990	Female	1+
120.	GNW	061-95473	09 Oct. 1990	Male	3+
121.	GBR	061-95470	09 Oct. 1990	Male	1+
122.	GBN	061-95474	10 Oct. 1990	Male	3+
123.	GBB	061-95477	10 Oct. 1990	Male	3+
124.	GBG	061-95482	15 Oct. 1990	Male	2+
125.	GBO	061-95480	13 Oct. 1990	Female	1+
126.	GBW	061-95483	15 Oct. 1990	Male	2+
127.	GGR	061-95484	16 Oct. 1990	Male	3+
128.	GGN	062-02137	11 Oct. 1991	Male	7+
129.	GGB	061-95488	18 Oct. 1990	Female	2+
130.	GGG	061-95489	18 Oct. 1990	Male	7+
131.	GGO	061-95490	19 Oct. 1990	Female	1+
132.	GGW	061-95493	22 Oct. 1990	Male	2+
133.	GOR	061-95500	11 Nov. 1990	Male	2+
134.	GON	062-02138	11 Oct. 1991	Female	2+
135.	GOB	062-02101	13 Nov. 1990	Male	2+
136.	GOG	062-02102	13 Nov. 1990	Female	2+
137.	GOO	062-02103	13 Nov. 1990	Female	2+
138.	GOW	062-02105	20 Nov. 1990	Female	2+
139.	GWR	061-95495	24 Oct. 1990	Male	2+
140.	GWN	062-02139	15 Oct. 1991	Male	4+
141.	GWB	061-95497	02 Nov. 1990	Male	2+
142.	GWG	061-95498	08 Nov. 1990	Male	3+

Colour band combination		Band number	Banding date	Sex	Age code (when banded)
143.	GWO	062-02109	29 Nov. 1990	Male	2+
144.	GWW	062-02104	14 Nov. 1990	Male	7+
145.	ORR	061-95451	22 Sep. 1990	Female	1+
146.	ORN	061-95452	22 Sep. 1990	Female	1+
147.	ORB	061-95457	28 Sep. 1990	Female	2+
148.	ORG	061-95458	28 Sep. 1990	Female	1+
149.	ORO	061-95459	28 Sep. 1990	Female	1+
150.	ORW	061-95460	30 Sep. 1990	Female	1+
151.	ONR	061-95464	03 Oct. 1990	Female	2+
152.	ONN	061-95465	03 Oct. 1990	Female	2+
153.	ONB	062-02146	24 Oct. 1991	Female	2+
154.	ONG	062-02252	08 Nov. 1991	Male	4+
155.	ONO	062-02253	08 Nov. 1991	Female	2+
156.	ONW	062-02254	12 Nov. 1991	Male	7+
157.	OBR	061-95471	09 Oct. 1990	Female	1+
158.	OBN	062-02256	16 Nov. 1991	Female	2+
159.	OBB	061-95472	09 Oct. 1990	Female	2+
160.	OBG	061-95475	10 Oct. 1990	Female	1+
161.	OBO	061-95476	10 Oct. 1990	Female	2+
162.	OBW	061-95478	12 Oct. 1990	Female	2+
163.	OGR	061-95479	12 Oct. 1990	Female	2+
164.	OGN	062-02257	19 Nov. 1991	Male	7+
165.	OGB	061-95481	14 Oct. 1990	Female	2+
166.	OGG	061-95485	16 Oct. 1990	Female	2+
167.	OGO	061-95486	18 Oct. 1990	Female	2+
168.	OGW	061-95487	18 Oct. 1990	Female	1+
169.	OOR	061-95491	19 Oct. 1990	Female	2+
170.	OON	062-02255	15 Nov. 1991	Female	3+
171.	OOB	061-95492	22 Oct. 1990	Female	2+
172.	OOG	061-95494	22 Oct. 1990	Female	2+
173.	OOO	061-95496	29 Oct. 1990	Female	2+
174.	OOW	061-95499	11 Nov. 1990	Female	2+
175.	OWR	062-02110	30 Nov. 1990	Female	2+
176.	OWN	062-02258	19 Nov. 1991	Male	6+
177.	OWB	062-02114	02 Sep. 1991	Male	2+
178.	OWG	062-02115	03 Sep. 1991	Female	1+
179.	OWO	062-02116	03 Sep. 1991	Female	2+
180.	OWW	062-02117	09 Sep. 1991	Female	1+
181.	WRR	062-02260	19 Nov. 1991	Male	4+
182.	WRN	062-02261	20 Nov. 1991	Male	7+
183.	WRB	062-02265	22 Nov. 1991	Male	6+
184.	WRG	062-02266	27 Nov. 1991	Male	7+
185.	WRO	062-02259	19 Nov. 1991	Female	3+

Colour band combination		Band number	Banding date	Sex	Age code (when banded)
186.	WRW	062-02267	28 Nov. 1991	Male	7+
187.	WNR	062-02269	30 Nov. 1991	Male	3+
188.	WNN	062-02274	03 Dec. 1991	Male	3+
189.	WNB	062-02277	19 Dec. 1991	Male	3+
190.	WNG	062-02278	23 Dec. 1991	Male	2+
191.	WNO	062-02262	20 Nov. 1991	Female	2+
192.	WNW	062-02279	29 Dec. 1991	Male	2+
193.	WBR	unused			
194.	WBN	unused			
195.	WBB	unused			
196.	WBG	unused			
197.	WBO	062-02263	20 Nov. 1991	Female	2+
198.	WBW	unused			
199.	WGR	062-02280	30 Dec. 1991	Male	2+
200.	WGN	062-02281	30 Dec. 1991	Male	3+
201.	WGB	unused			
202.	WGG	unused			
203.	WGO	062-02264	20 Nov. 1991	Female	2+
204.	WGW	unused			
205.	WOR	062-02268	30 Nov. 1991	Female	1+
206.	WON	062-02270	01 Dec. 1991	Female	2+
207.	WOB	062-02271	03 Dec. 1991	Female	2+
208.	WOG	062-02272	03 Dec. 1991	Female	2+
209.	WOO	062-02273	03 Dec. 1991	Female	2+
210.	WOW	062-02275	04 Dec. 1991	Female	3+
211.	WWR	unused			
212.	WWN	unused			
213.	WWB	unused			
214.	WWG	unused			
215.	WWO	062-02276	16 Dec. 1991	Male	2+
216.	WWW	unused			

Appendix 4: Museum specimens

A total of 433 *Sericulus* specimens was examined in zoological collections in Australia and Europe: 86 specimens of Flame Bowerbirds, 15 of the southern taxon *ardens* (= *ard.*) and 71 of the northern taxon *aureus* (= *aur.*), 346 specimens of Regent Bowerbirds (= *chr.*) and 1 specimen of the Fire-maned Bowerbird (AM O.42549).

Collection	*ard.*	*aur.*	*chr.*
AM = Australian Museum (Sydney, Australia)	1	0	120
ANWC = Australian National Wildlife Collection (CSIRO, Commonwealth Scientific and Industrial Research Organization, Division of Wildlife and Ecology, Canberra, Australia)	0	0	14
BMNH = British Museum (Natural History) (Sub-department of Ornithology, Tring, United Kingdom)	6	11	34
MHN = Museum National d'Histoire Naturelle (Paris, France)	0	5	20
MV = Museum of Victoria (Melbourne, Australia)	0	1	16
MVHLW = H.L. White Collection (kept in the Museum of Victoria, Melbourne, Australia)	0	0	24
NRS = Naturhistoriska Riksmuseet/ Swedish Museum of Natural History (Stockholm, Sweden)	0	3	0
QM = Queensland Museum (Brisbane, Australia)	2	0	66
RMNH/NNM = Rijksmuseum van Natuurlijke Historie/ National Museum of Natural History (Leiden, the Netherlands)	4	21	8
SMF = Forschungsinstitut und Natur-Museum Senckenberg (Frankfurt am Main, Germany)	0	14	6
SMNS = Staatliches Museum für Naturkunde Stuttgart (Stuttgart, Germany)	0	8	17
SMT = Staatliches Museum für Tierkunde (Dresden, Germany)	0	1	6
WMM = Westfälisches Museum für Naturkunde (Münster, Germany)	0	1	0
ZMB = Zoologisches Museum Berlin (Berlin, Germany)	2	3	5
ZMH = Zoologisches Museum Hamburg (Hamburg, Germany)	0	0	6
ZMK = Zoologisches Museum Kiel (Kiel, Germany)	0	1	2
ZSM = Zoologische Staatssammlung München (München, Germany)	0	2	2
Total	15	71	346

Appendix 5: ABBBS banding data

The Australian Bird and Bat Banding Schemes ABBBS (Australian National Parks and Wildlife Service, Canberra) provided not yet analysed morphometric measurements of 361 Regent Bowerbirds and data of 127 re-traps. The data contribution of the bird banders listed is gratefully acknowledged.

Authority number	Bander's name	Number of birds measured	Number of re-traps
84	Mr. S.G. Lane	94	14
102	Mr. R.G. Lonnon	21	0
123	Mr. H. Battam	0	1
154	Mr. S.J. Wilson	0	4
217	Mr. H.J. de S. Disney	6	0
250	Mr. P.D. Strong	0	9
265	Mr. R. Lossin	0	1
298	Mr. R. Elks	0	1
306	Mr. C.S. Day	0	2
328	Mr. R.J. Smith	0	13
378	Dr. R.H. Donaghey	16	1
420	Mr. G.B. Baker	1	0
455	Dr. G.R. Cam	2	0
536	Mr. G.P. Clancy	43	23
554	Mr. G.J. Logan	4	0
555	Mr. F.W.C. van Gessel	46	11
580	Ms. A.E. Cam	2	0
637	Mr. P.A. White	26	13
656	Mr. A.J. Leishman	3	2
664	Mr. D.I. Smedley	17	20
720	Mr. J.S. McCrea	0	1
771	Mr. D.L. Binns	67	11
852	Mr. J.W. Hardy	3	0
1090	Mr. G.D. Bell	5	0
1096	Mr. D.J. Geering	5	0
Total		361	127

Appendix 6: Taxonomy of the genus *Sericulus*

Based on the evidence of geographical variation of the genus *Sericulus* analysed in Chapter 3, the genus contains the following four species:

Sericulus aureus (LINNÉ 1758)
Northern Flame Bowerbird, Nördlicher Goldlaubenvogel
[*Xanthomelus aureus*, Systema Naturae, 10th edn., p. 108]

Sericulus ardens (D'ALBERTIS & SALVADORI 1879)
Southern Flame Bowerbird, Südlicher Goldlaubenvogel
[*Xanthomelus ardens*, Annal Museo Civico Genova 1st ser. 14, p. 113]

Sericulus bakeri (CHAPIN 1929)
Fire-maned Bowerbird, Rotscheitel-Laubenvogel
[*Xanthomelus bakeri*, American Museum Novitates 367, p. 1]

Sericulus chrysocephalus (LEWIN 1808)
Regent Bowerbird, Gelbnacken-Laubenvogel
[*Meliphaga chrysocephala*, Birds of New Holland, Sydney, pl. 6, p. 10]

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Plate 1. Spotted Catbird *Ailuroedus melanotis*, representative of the only bowerbird genus that does not build display courts (Atherton Tableland, NE Queensland, 10 April 1992). - **Tafel 1.** Schwarzohr-Katzenvogel *Ailuroedus melanotis*, Vertreter der einzigen Laubenvogelgattung, die keine Balzplätze errichtet.

Plate 2. Court of a Tooth-billed Bowerbird *Scenopoeetes dentirostris*, decorated with leaves laid paler side uppermost (Atherton Tableland, NE Queensland, 20 September 1992). - **Tafel 2.** Tenne eines Zahnlaubenvogels *Scenopoeetes dentirostris*, dekoriert mit Blättern, die mit der helleren Unterseite nach oben gelegt wurden.

Plate 3. Mat bower of an Archbold's Bowerbird *Archboldia papuensis* (Tari Gap, Southern Highlands, Papua New Guinea, 21 August 1990). - **Tafel 3.** Mattenlaube eines Archboldlaubenvogels *Archboldia papuensis.*

Plate 4. Part of an occipital plume of a male King of Saxony Bird of Paradise *Pteridophora alberti* as bower decoration of an Archbold's Bowerbird (Tari Gap, Southern Highlands, Papua New Guinea, 21 August 1990). - **Tafel 4.** Teil einer Hinterkopf-Schmuckfeder eines männlichen Wimpelträgers *Pteridophora alberti* als Laubendekorationsobjekt eines Archboldlaubenvogels.

Plate 5. Maypole bower of a Golden Bowerbird *Prionodura newtoniana* (Atherton Tableland, NE Queensland, 7 April 1992). - **Tafel 5.** Maibaumlaube eines Säulengärtners *Prionodura newtoniana*.

Plate 6. Avenue bower of a Satin Bowerbird *Ptilonorhynchus violaceus* with blue feathers of Crimson Rosellas *Platycercus elegans* as bower decoration (Green Mountains, SE Queensland, 10 December 1993). - **Tafel 6.** Alleelaube eines Seidenlaubenvogels *Ptilonorhynchus violaceus* mit blauen Federn von Pennantsittichen *Platycercus elegans* als Laubendekoration.

Plate 7. Adult male Satin Bowerbird (Green Mountains, SE Queensland, 9 December 1993). - **Tafel 7.** Adulter männlicher Seidenlaubenvogel.

Plate 8. Female Satin Bowerbird visiting a bower; adult male bower owner performing display on the left (Green Mountains, SE Queensland, 11 December 1993). - **Tafel 8.** Weiblicher Seidenlaubenvogel beim Laubenbesuch; der adulte männliche Laubenbesitzer balzt links von der Laube.

Plate 9. Well-constructed and highly-decorated bower (including many man-made objects) of an adult male Satin Bowerbird; bower owner sitting in the avenue (Green Mountains, SE Queensland, 20 October 1985). - **Tafel 9.** Gut gebaute und stark dekorierte Laube (darunter viele Objekte menschlicher Herkunft) eines adulten männlichen Seidenlaubenvogels; der Laubenbesitzer sitzt in der Allee.

Plate 10. Less decorated bower of an immature male Satin Bowerbird (Green Mountains, SE Queensland, 22 September 1989). - **Tafel 10.** Weniger stark dekorierte Laube eines immaturen männlichen Seidenlaubenvogels.

Plate 11. Adult male Regent Bowerbird *Sericulus chrysocephalus* (Green Mountains, SE Queensland, 26 November 1991). - **Tafel 11.** Adulter männlicher Gelbnacken-Laubenvogel *Sericulus chrysocephalus*.

Plate 12. Avenue bower of a Regent Bowerbird (Sarabah Range, SE Queensland, 8 October 1989). - **Tafel 12.** Alleelaube eines Gelbnacken-Laubenvogels.

Plate 13. Adult male Spotted Bowerbird *Chlamydera maculata* (Cape River, Central Queensland, 20 October 1995). - **Tafel 13.** Adulter männlicher Östlicher Fleckenlaubenvogel *Chlamydera maculata*.

Plate 14. Avenue bower of a Spotted Bowerbird (Cape River, Central Queensland, 20 October 1995). - **Tafel 14.** Alleelaube eines Östlichen Fleckenlaubenvogels.

Plate 15. Avenue bower of a Great Bowerbird *Chlamydera nuchalis* (Atherton Tableland, NE Queensland, 10 April 1992). - **Tafel 15.** Alleelaube eines Graulaubenvogels *Chlamydera nuchalis*.

Plate 16. Avenue bower of a Fawn-breasted Bowerbird *Chlamydera cerviniventris* (Cape York, N Queensland, 17 November 1993). - **Tafel 16.** Alleelaube eines Braunbauch-Laubenvogels *Chlamydera cerviniventris*.

Plate 17. Dry rainforest with Hoop Pines *Araucaria cunninghamii*, habitat for the Regent Bowerbird (view over Canungra Creek Valley, Sarabah Range, SE Queensland, 14 January 1990). - **Tafel 17.** Trockenregenwald mit Araukarien der Art *Araucaria cunninghamii*, Habitat für den Gelbnacken-Laubenvogel (Blick auf das Tal des Canungra Creek).

Plate 18. Dry rainforest with emergent Deciduous Fig *Ficus superba* var. *henneana*, habitat for the Regent Bowerbird (Sarabah Range, SE Queensland, 7 November 1989). - **Tafel 18.** Trockenregenwald mit herausragender Feige der Art *Ficus superba* var. *henneana*, Habitat für den Gelbnacken-Laubenvogel.

Plate 19. Female Regent Bowerbird (Green Mountains, SE Queensland, 26 November 1991). - **Tafel 19.** Weiblicher Gelbnacken-Laubenvogel.

Plate 20. Immature male Regent Bowerbird, at least two years old; iris mottled with yellowish spots, bill blackish (Green Mountains, SE Queensland, 1 September 1989). - **Tafel 20.** Immaturer männlicher Gelbnacken-Laubenvogel, mindestens zwei Jahre alt; Iris mit gelblichen Flecken gesprenkelt, Schnabel schwärzlich.

Plate 21. Subadult male Regent Bowerbird, c. three years old; iris largely yellowish, bill with some orange at the base (Green Mountains, SE Queensland, 30 July 1989). - **Tafel 21.** Subadulter männlicher Gelbnacken-Laubenvogel, ca. drei Jahre alt; Iris weitgehend gelblich, Schnabel mit etwas orange an der Wurzel.

Plate 22. Subadult male Regent Bowerbird, c. four years old; iris yellow, bill largely orange (Green Mountains, SE Queensland, 22 August 1989). - **Tafel 22.** Subadulter männlicher Gelbnacken-Laubenvogel, ca. vier Jahre alt; Iris gelb, Schnabel weitgehend orange.

Plate 23. Subadult male Regent Bowerbird, c. five years old; iris yellow, bill orange (Green Mountains, SE Queensland, 26 November 1991). - **Tafel 23.** Subadulter männlicher Gelbnacken-Laubenvogel, ca. fünf Jahre alt; Iris gelb, Schnabel orange.

Plate 24. Subadult male Regent Bowerbird, c. five to six years old; iris yellow, bill orange, only head with largely adult plumage (Green Mountains, SE Queensland, 28 July 1989). - **Tafel 24.** Subadulter männlicher Gelbnacken-Laubenvogel, ca. fünf bis sechs Jahre alt; Iris gelb, Schnabel orange, nur der Kopf mit weitgehend adultem Gefieder.

Plate 25. Adult male Regent Bowerbird, at least six years old (Green Mountains, SE Queensland, 22 August 1989). - **Tafel 25.** Adulter männlicher Gelbnacken-Laubenvogel, mindestens sechs Jahre alt.

Plate 26. Adult male and female Flame Bowerbird *Sericulus (aureus) ardens* (southern taxon) from the Endrich River, Irian Jaya, New Guinea (specimens O.3432 and O.3433, Queensland Museum, Brisbane, 18 February 1991). - **Tafel 26.** Adulter männlicher und weiblicher Goldlaubenvogel *Sericulus (aureus) ardens* (südliches Taxon) vom Endrich River, Irian Jaya, Neuguinea (Bälge O.3432 und O.3433, Queensland Museum).

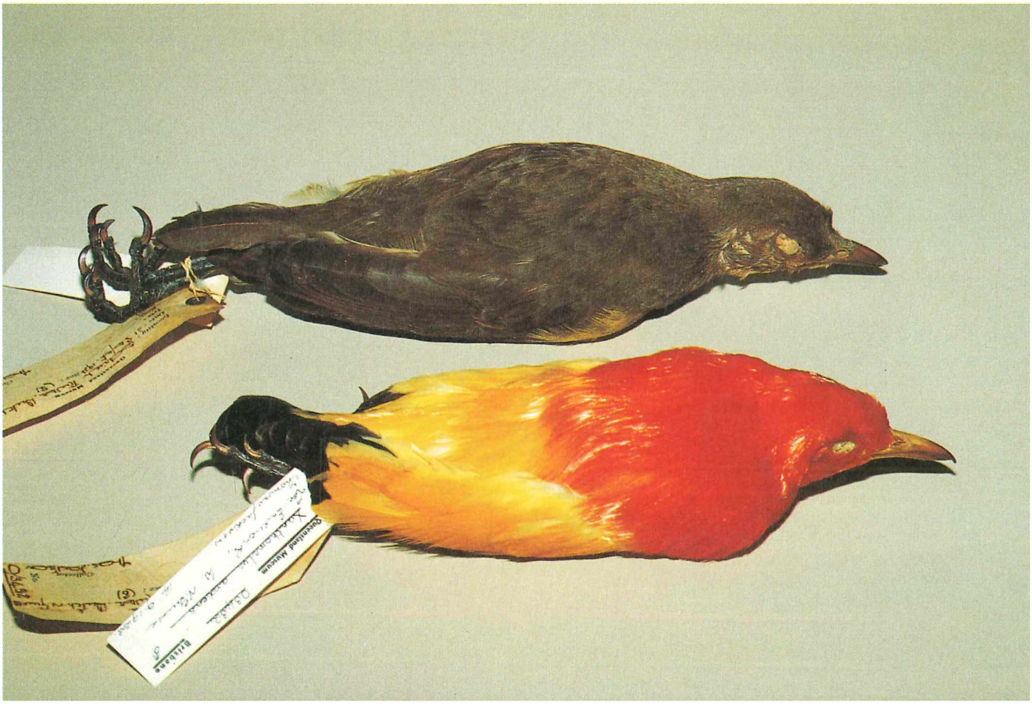

Plate 27. Bower sites of Regent Bowerbirds are characterized by a large percentage of liana-thicket cover (Sarabah Range, SE Queensland, 1 December 1989). - **Tafel 27.** Laubenplätze von Gelbnacken-Laubenvögeln sind durch einen großen Anteil an Lianendickicht gekennzeichnet.

Plate 28. Avenue bower of an adult male Regent Bowerbird, consisting of densely-packed sticks; decoration objects are a fresh green leaf, brown fruit of Deep Yellow-wood *Rhodosphaera rhodanthema*, and snail shells (Sarabah Range, SE Queensland, 17 November 1989). - **Tafel 28.** Alleelaube eines adulten männlichen Gelbnacken-Laubenvogels, aus dicht zusammengefügten Stöckchen bestehend; Dekorationsobjekte sind ein frisches grünes Blatt, braune Früchte des Sumachgewächses *Rhodosphaera rhodanthema* und Schneckengehäuse.

Plate 29. Avenue bower of an adult male Regent Bowerbird, consisting of rather loosely-inserted sticks; decoration objects as on Plate 28 (Sarabah Range, SE Queensland, 14 November 1990). - **Tafel 29.** Alleelaube eines adulten männlichen Gelbnacken-Laubenvogels, aus eher lose eingefügten Stöckchen bestehend; Dekorationsobjekte wie auf Tafel 28.

Plate 30. Avenue bower of a subadult male Regent Bowerbird (Sarabah Range, SE Queensland, 26 December 1990). - **Tafel 30.** Alleelaube eines subadulten männlichen Gelbnacken-Laubenvogels.

Plate 31. Adult male Regent Bowerbird (colour band combination RGW) masticating a leaf for bower painting (Sarabah Range, SE Queensland, 17 October 1991). - **Tafel 31.** Adulter männlicher Gelbnacken-Laubenvogel (Farbringkombination RGW) beim Zerkauen eines Blattes zum Bemalen der Laube.

Plate 32. Adult male Regent Bowerbird (colour band combination RNR) stealing a snail shell from the bower of a neighbouring male (Sarabah Range, SE Queensland, 19 October 1991). - **Tafel 32.** Adulter männlicher Gelbnacken-Laubenvogel (Farbringkombination RNR) beim Stehlen eines Schneckengehäuses von der Laube eines benachbarten Männchens.
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