AN ASSESSMENT OF MALE PARENTAL INVESTMENT AND PAIR BONDING IN THE POLYGAMOUS SUPERB LYREBIRD

ALAN LILL

Departments of Zoology and Psychology, Monash University, Clayton, Victoria, Australia 3168

ABSTRACT.—The extent of paternal investment and pair-bonding in two southeast Australian populations of polygamous Superb Lyrebirds (*Menura superba*) was studied over 6 yr. Male visits to nests during both my prolonged, concealed observations and brief, unconcealed inspections were rare. The few visits seen were either incidental to foraging or induced by observer disturbance, and no male anti-nest predator behavior occurred. Because males do not rear young, they are thus totally emancipated from a parental care role.

Solitary adult males and female-plumaged birds comprised 71% of the 585 sightings of lyrebird social units obtained. Single adult males and female-plumaged birds that I pursued for long periods contacted opposite-sexed birds infrequently and briefly. Male courtship display was common during these contacts, but females were mostly unresponsive. Some females' breeding territories overlapped those of more than one male, and one female well established on such a territory visited at least two displaying males prior to mating. Some females and males made extra-territorial courtship excursions. Collectively these observations suggest that pair bonding does not occur or involves a very limited time commitment.

The lack of paternal care and limited time and energy expenditure in heterosexual association are thought to be significant in relation to the criteria used in mate-choice, the intensity of sexual selection, and males' ability to exploit the environmental polygamy potential. *Received 14 August 1978, accepted 13 February 1979.*

THE Superb Lyrebird, *Menura superba*, is a large, mainly cursorial passerine inhabiting chiefly the wet forests of southeast Australia. It eats mainly soil invertebrates and breeds in winter. Adult males clear many raised earth display mounds in their large territories, on and near to which they sing extensively in the breeding season. Their song contains a high proportion of interspecific mimicry. Courtship of females may begin away from the mounds with Whisper-song (Kenyon 1972), subdued singing with accompanying wing and tail movements. It culminates in an elaborate "dance" on a mound, in which the male's modified retrices are spread forward over the head in a vibrating fan configuration. Copulation is probably restricted to the mounds. Females occupy smaller territories, build large, domed nests often situated on the ground, breed once per year, and typically lay a single-egg clutch. Incubation and nestling development take 14 weeks and post-fledging parental care lasts several months. Rowley (1975) has summarized the species' breeding biology.

Contrary to earlier claims (Campbell 1941, Chisholm 1960), Kenyon (1972) proved that lyrebirds are polygamous by showing that an identified male copulated with several hens in each of three breeding seasons. Reilly (1970) established that males are not involved in nest-building, incubation, or feeding nestlings and fledglings. The type of polygamy shown by Superb Lyrebirds, however, remains unclear. The main alternatives are (a) promiscuity, in which successful males copulate with two or more females, either forming no pair bonds with them or very brief ones; paternal care is typically lacking; or (b) polygyny, in which successful males form durable pair bonds either simultaneously or successively with several females with whom they copulate exclusively; some paternal care usually occurs (Selander 1972).

Reilly (1970) implied the existence of limited paternal care in lyrebirds by claiming

that males were aware of nest locations and sometimes defended nests. Kenyon (1972) argued that "the possibility of lyrebirds being promiscuous is extremely remote," and that their mating system involved simultaneous polygyny with long-term pair-bonding. In addition to Reilly's (1970) claim, Kenyon's argument stemmed from three observations: (a) the single territorial male he studied courted and copulated with one particular hen in two successive seasons and with another in three, (b) its territory enclosed those of three hens it copulated with, and (c) it frequently fed within 10 m of these hens. But these observations, even if typical of lyrebirds generally, do not unequivocally suggest polygyny rather than promiscuity (Rowley 1975).

Accurate classification of the mating system, however, is relatively unimportant. But determining the extent of paternal care and pair bonding is an important step in understanding the evolution of polygamy in lyrebirds. Imbalanced parental investment ratios lead to increased variance in mating success in the limited sex and thus probably to more intense sexual selection (Trivers 1972). Moreover, a male's ability to capitalize on any environmental potential for mate monopolization will be strongly influenced by his time and energy investment in parental and pair bonding behavior (Emlen and Oring 1977). Many aspects of the Superb Lyrebird's behavior and ecology (e.g. "shyness," rapid locomotion, use of many dispersed mating sites, and densely vegetated habitat) make detailed documentation of the mating distribution almost impossible. Here I present some less direct evidence that helps to elucidate the extent of paternal care and pair formation in lyrebirds.

STUDY AREAS AND METHODS

Two main sites were used in the 6-yr study. Sherbrooke Forest Park is a 4,942-ha mature wet sclerophyll (Mountain Ash, *Eucalyptus regnans*) forest reserve 37 km east of Melbourne (37°45'S, 144°58'E). Unlike most lyrebirds, many Sherbrooke birds are very tame due to prolonged, nonviolent contact with people (Rowley 1975). Most of my work was done in a little-frequented part of the reserve, however, where many birds were less approachable. Several birds were color-banded and several others were morphologically distinct. The second area, Maroondah Catchment Area, is a forested tract of the Great Dividing Range near Healesville, 57 km northeast of Melbourne. I worked in mature *E. regnans* forest on Mt. Riddell and in mixed-eucalypt forest at Fernshaw. Human access was limited, and lyrebirds were hard to observe except from concealment. A few observations were also made in wet sclerophyll forest near Powelltown, 70 km east of Melbourne.

Data were gathered in several ways and are grouped under three headings: the extent of paternal care, the extent of pair bonding, and mate selection and adult territorial dispersion.

The extent of paternal care.—To see if paternal care occurred, I recorded the frequency and nature of male visits to active nests during brief (a few seconds to 5 min), unconcealed visits I paid to nests to check visually and sometimes measure contents, and during prolonged (22–600 min), concealed watches I made from blinds.

The extent of pair bonding.—To determine whether pair formation occurred, I recorded the frequency and nature of social contacts (other than at nests and mounds) made with unlike-sex-plumaged birds by single adult males and single female-plumaged (FP) birds that I followed continuously for 6–355 min ($\bar{x}$ = 142 min) periods. These observations I have called "pursuits." A social contact involved approach to within 25 m of unlike-sex-plumaged individuals with or without ensuing interaction. Note that due to sexual bimaturism (Wiley 1974), females and young males have similar plumage and are referred to throughout as female-plumaged birds or FPs. Pursuit data pertain only to tamer Sherbrooke birds, so I feel confident my pursuit influenced contact frequency minimally. I also recorded the relative frequencies at which solitary males, solitary FPs, and heterosexual groups featured in all clear sightings of lyrebird social units obtained during the study. Behavioral interactions in such units were recorded where possible.

Mate selection and adult territorial dispersion.—The territorial dispersion of adult males and females in a 72-ha plot in Sherbrooke Forest was documented over 2 yr by plotting sightings of, and routes used

Fig. 1.   A nesting female threatens the author during a brief nest inspection at the nestling stage.

by, identified birds on sketch maps. Sexual interactions of identified birds were recorded opportunistically in this area over the same period. The plot contained four male and at least seven female territories.

RESULTS

The extent of paternal care.—Males do not build nests or raise young, so any paternal care would probably involve anti-nest predator behavior and/or "guaranteeing" food resources for the breeding unit through territoriality. The latter possibility is discussed on p. 496. To assess whether adult males protect nest contents against predators, one must know how often and in what circumstances they visit nests and what behavior they exhibit there.

A male arrived (i.e. approached within 25 m) at the nest during only 6 of 789 brief inspections (incubation = 476, nestling stage = 313 inspections) I made of 67 nests over 6 seasons. Males arrived significantly more often when the hen was present but off the nest than when she was absent, present only momentarily before fleeing, or sitting silently and undisturbed in her nest (1.94% of occasions vs. 0%; $\chi_1^2 = 5.984$, $P < 0.05$). This was probably because the stimulus eliciting male approach was maternal alarm calling. But though this was more frequent and intense during my nestling than my egg inspections, males did not approach nests more often during nestling inspections (1.6% of occasions vs. 0.21%; $\chi_1^2 = 3.153$, $P > 0.05$). Of a sample of 232 inspections in which maternal alarm calling was noted, only 1.3% were characterized by male approach. It is thus probable that males that happened to be foraging near nests on their territories were more likely to approach

TABLE 1. Frequencies at which single, pursued adult males and female-plumaged birds made heterosexual social contacts away from mounds and nests in Sherbrooke Forest, 1973–1976.

	Total h pursued	Number of pursuits	Contacts[a] with single FPs	Contacts with FP[b] groups	Season
Males (4 identified and 1 unidentified)	107.6	46	11	3	Breeding (May–November)
Males (2 identified and >1 unidentified)	45.8	20	6	3	Non-breeding (December–April)

	Total h pursued	Number of pursuits	Contacts with single adult males	Contacts with adult male groups	Season
Female-plumaged birds (5 identified hens and >1 unidentified FP)	120.3	45	6	0	Breeding
Female-plumaged birds (2 identified hens and >1 unidentified FP)	43.9	20	4	0	Non-breeding

[a] A social contact occurred when a pursued bird came within 25 m of one or a group of birds of apparently different gender.
[b] FP = female-plumaged (see text).

them during my inspections if the nesting hen was present and vocal than if she was absent or present but silent. But the very low male approach rate is clearly not indicative of effective male anti-nest predator behavior.

Nesting hens frequently threatened me throughout my brief inspection from as little as 1 m away (Fig. 1), and they sometimes attacked me; no attracted male came nearer than 7 m, and most remained much farther away. All the males left spontaneously while I was still at the nest, but the mother (and often her nestling) continued to threaten me. On three occasions the attracted male courted the nesting hen, but no male was aggressive to me or exhibited decoy behavior.

During 261.9 h of prolonged observation from blinds at 22 nests over 5 breeding seasons, I saw males only 7 times. No sightings occurred during nest building (20.1 h observation), four during incubation (106.9 h), and three during the nestling stage (134.9 h). Three sightings occurred at one nest and the others at four separate nests. In 5 of the 7 sightings, a male simply passed 20–25 m from the nest while foraging; on 4 of these occasions the males did not orient to the nest although twice the hen was sitting. On the fifth occasion a foraging male paused briefly to emit one species-typical song 20 m from the untenanted nest, but males do this throughout their territories. The sixth sighting was of a male passing 2 m from a nest during the hen's absence without even looking at it. In the seventh sighting, a male sang and preened extensively, after descent from its nocturnal roost, 10 m from a nest containing a chick; the mother was absent, and the male did not orientate to the nest. Additionally, no males visited nine nests during 39.5 h of unconcealed observations I made at all stages of nesting.

Thus the rare visits of males to nest sites were incidental to foraging or elicited by observer-induced disturbance. Visiting males exhibited no anti-predator behavior toward me.

The extent of pair bonding.—Pair bonding usually entails not only an exclusive

TABLE 2. Frequencies at which Superb Lyrebirds were sighted alone or associating with apparently different-sexed birds at both study areas, 1973–1978. Numbers in parentheses are percentages of total sightings in which known females were involved. Percentages in rows do not total 100%, as apparently unisexual groups are included in the total number of sightings but not in the percentage composition figures.

Season	Total sightings[a]	Percentage of sightings comprising			
		Solitary adult males[b]	Solitary FPs[c]	One adult male and one FP	Heterosexual groups[d] or more than two birds
Breeding	406	40	36 (10)	8 (4)	3 (0.3)
Non-breeding	179	35	32 (9)	10 (3)	6 (0.6)
Both	585	37	35 (10)	9 (3)	4 (0.3)

[a] A sighting is an initial observation of a bird or group of birds.
[b] The category "adult male" includes sub-adult males with partially adult-type tail feathers.
[c] FPs are female-plumaged birds.
[d] "Heterosexual groups" probably include many social units in which all FPs were juvenile males.

sexual relationship but also extensive association between the bonded birds (Hinde 1964). Thus polygynous male birds typically spend considerable time and energy associating and interacting with their mates (e.g. Dickcissel, *Spiza americana*; Zimmerman 1966), even when paternal care is limited. To help decide whether lyrebirds form pair bonds, I recorded the frequency and nature of their heterosexual association.

Table 1 shows how often single territorial males and single FPs that I pursued for long periods made heterosexual contacts other than at mounds and nests in Sherbrooke Forest. Members of FP groups contacted by adult males were assumed from their behavior to be immature males. Therefore, pursued males contacted a known or suspected female once per 9.8 pursuit-h in the breeding season and once per 7.6 pursuit-h in the non-breeding season, when they were more mobile on their territories. Single pursued FPs contacted single adult males once per 20.1 pursuit-h on average in the breeding season and once in 10.9 pursuit-h outside the breeding season. Most of these contacts between single adult males and single FPs were brief.

Table 2 lists the relative frequencies at which solitary birds and heterosexual groups were sighted (other than at nests) at Sherbrooke and Maroondah. Solitary males and solitary FPs were the most commonly observed social "units," jointly comprising 76% of breeding season sightings and 67% of those obtained in the non-breeding season. As indicated above, FP groups contained mostly immature males, so the relative sighting frequency of one male-one FP units is the best indicator of association levels between territorial cocks and hens away from nests. Such dyads comprised only 8–10% of the sightings, the proportion not differing significantly between breeding and non-breeding seasons ($\chi_1^2 = 0.001$, $P > 0.05$).

I was able to document the form of 60 single male-single FP social contacts during the study (Table 3). Of these contacts, 16% during the breeding season and 36% during the non-breeding season lacked overt interaction; a further 3% of breeding season contacts and 7% of non-breeding season ones involved no more than approach responses by one or both birds. All the other contacts included male courtship display (mainly Whisper-song) to which females were mostly unresponsive. In a (not necessarily unbiased) sample of 28 one male-one FP contacts from the breeding and non-breeding seasons, 22 lasted <5 min and 6 lasted >5 min. The percentage lasting over 5 min was not significantly greater in the breeding than the non-breeding season

TABLE 3. The form of social contacts between single adult males and female-plumaged birds occurring away from mating sites and nests at both study areas, 1973–1976.

Contact type[a]	Heterosexual group composition			
	Breeding season		Non-breeding season	
	Male + 1 FP[b]	Male + >1 FP	Male + 1 FP	Male + >1 FP
Sexes passed or fed within 25 m but no interaction	5 (2)	0	5 (2)	0
One or both sexes approached only[c]	1 (0)	0	1 (0)	1 (0)
Male displayed → FP(s) approached	5 (0)	0	0	0
Male displayed → FP(s) threatened	0	0	1 (1)	1 (0)
Male displayed → FP(s) fled	0	0	2 (1)	0
Male displayed → no overt FP response	21 (11)	1 (1)	5 (1)	2 (0)
Male displayed → FPs mutually aggressive	—	6 (0)	—	3 (1)

[a] A social contact is as defined under Methods. Numbers in parentheses indicated contacts in which birds known to be females were involved.
[b] FP = female-plumaged bird.
[c] "Approached only" covers cases where either the male, the FP bird(s) or both deviated from their previous track to approach the contacted individual(s); "passed or fed within 25 m" involved no such deviation.

(23.5% vs. 18.2%, $P > 0.05$, Fisher test). The FP groups contacted by adult males contained mainly immature males that were mutually aggressive but usually unresponsive to the adult birds.

These results show that heterosexual association away from display mounds was infrequent, brief, and generally devoid of reciprocal interaction.

Mate selection and adult territorial dispersion.—If lyrebirds typically form pair bonds lasting several years, as implied by Kenyon (1972), females well established on territories should not extensively "sample" potential mates each breeding season unless their previous mate disappeared. Such sampling would be predicted, however, in polygynous species with pair bonds lasting only one season and in promiscuous species. Indeed, Lill (1974, 1976) and Payne and Payne (1977) have documented such behavior in promiscuous manakins and viduine finches.

Polygyny implies some level of paternal care, even if it is limited to provision of resources for offspring through territoriality. But clearly a polygynous male should normally care only for his own offspring. This can be ensured either by guarding mates or defending their breeding territories during the period in which mates can be fertilized. Direct guarding of receptive hens clearly did not occur in the study populations (see previous section), leaving defense of female breeding territories as the only alternative anti-cuckoldry strategy for polygynous males. If male lyrebirds are indeed polygynous, this strategy should be reflected in the spatial relationship of male and female territories.

Several females' nesting territories, however, overlapped those of more than one male (Fig. 2). Female S's territory overlapped those of males M3 and M4, for example. She was identified in the 1974 breeding season, but had probably occupied her territory since the previous non-breeding season. An incomplete protocol of her sexual behavior shows she was courted by both males in the 1974/75 non-breeding season and in the weeks prior to laying in 1975:

July–August 1974.—Nested unsuccessfully in M3's core area but close to M3/M4 territorial overlap zone (Fig. 2). Her sexual interactions unknown.

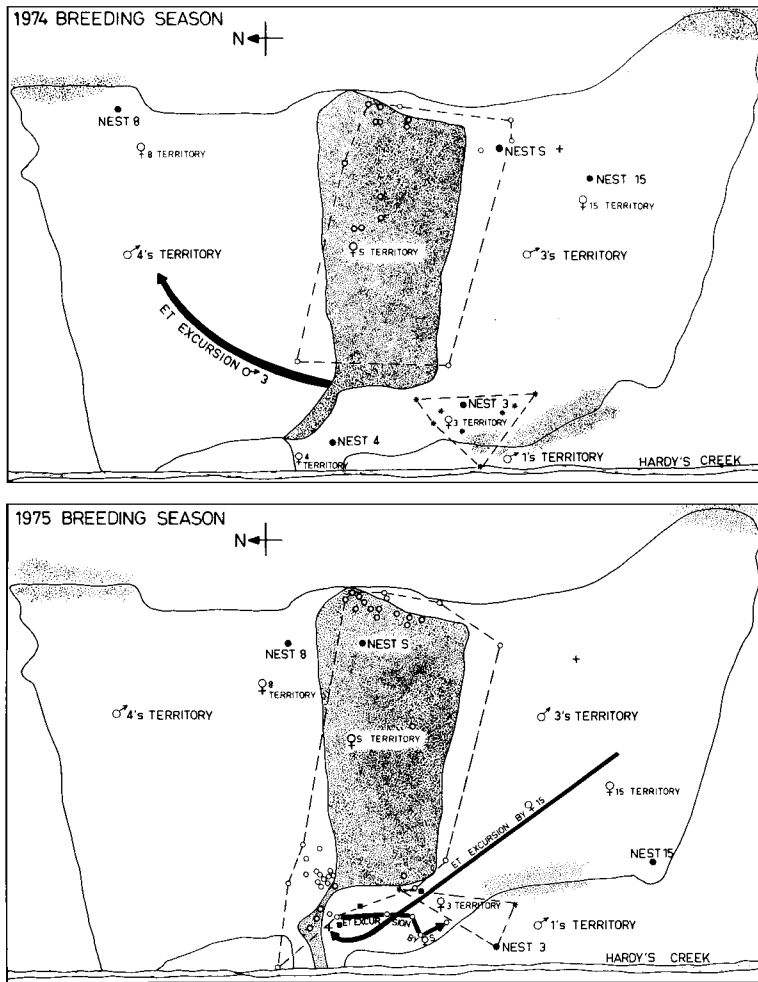4 December 1974.—Courted by M4 in his core area—she threatened and avoided him.

Fig. 2.   Spatial dispersion of male and female lyrebird territories in a small area of Sherbrooke Forest in 1974 and 1975. Solid lines indicate the boundaries of male territories, while overlap zones between adjacent male territories are stippled. The ♂3/♂4 zone is exactly plotted, while other overlap zones are indicated by unbounded stippling. The dashed lines indicate minimal convex polygons linking the outermost sightings of Females S and 3, except for the western end of S's territory in 1975, which is more exactly indicated. ○ = locations where Female S was sighted or which she visited while being pursued (multiple sightings were made at many of these locations); + = sightings of Female 15; ■ = sightings of a hen whose territory lay outside Male 3's and off the area of the map; * = sightings of Female 3; ET excursion = extra-territorial courtship excursion.

17 December 1974.—Social contact lacking overt interaction with M4 in M3/M4 overlap zone.

23 December 1974.—Two contacts with M4; unresponsive to male's singing in one encounter.

18 February 1975.—Courted by M3 while with an FP group in his core area—unresponsive but aggressive to other FPs (probably immature males).

11 and 23 May 1975.—Courted by M3 in M3/M4 overlap zone.

2–19 June 1975.—Courted by M4 on 3 days and had non-courtship contacts with him on two others.

24 June–24 August 1975.—Courted by M3 at and away from his mounds on 5 days; one of her mound visits involved an extra-territorial excursion. Layed in early July in nest in M3/M4 overlap zone. Courted by M3 pre-laying, during incubation, and after nest failure.

M3 had been established on his territory at least since the 1973 breeding season and M4 on his at least since the following one.

Other fragmentary observations indicate that such "mate-sampling" behavior may not be restricted to hens with overlapping territories. Some females moved off their territories to visit displaying males; thus M3 courted a hen whose territory did not overlap his at all, and two hens made extra-territorial trips to visit a displaying male whose territory their own partly overlapped. Occasionally cocks made similar excursions deep into neighboring males' territories while courting FPs that had visited them at their main mounds (Fig. 2). These findings shed some doubt on the existence of long-term pair bonds and resource defense polygyny in Superb Lyrebirds.

DISCUSSION

The extent of paternal care.—Efficient male anti-nest predator behavior would require (a) considerable nest surveillance, (b) a high level of responsiveness to nestling and maternal alarm signals, and (c) predator-oriented aggression or decoy behavior at endangered nests. Observations from blinds showed that males rarely visited nests in the effective absence of people. Even two visits by potential nest predators (a fox, *Vulpes vulpes,* and a Red-bellied Black Snake, *Pseudechis porphyriacus*) failed to attract a male despite conspicuous maternal alarm calls. The few male visits seen from concealment were mostly incidental to foraging, and the males did not orient to the nest even when the hen was present. Male visits to nests were also rare during my brief, unconcealed inspections, despite frequent alarm responses by the nesting females; attracted males showed neither aggression nor decoy behavior toward me. Thus the prerequisites for effective nest protection by males were not evident.

The extensive overlap of male and female territories made it inevitable that foraging males would occasionally pass close to nests during my concealed observations and unconcealed inspections. Approach without subsequent anti-predator behavior is quite a common avian response to certain types of alarm and "distress" calls. That a few sightings of males near nests were obtained during my brief inspections is thus not surprising, and most similar reported sightings were made in the presence of unconcealed observers (Edwards 1919, Tregallas 1921, W. B. A. 1925, Leach 1929, Campbell 1941, Reilly 1970). Attracted males sometimes courted the nesting hen. The agonistic and courtship display repertoires of *Menura superba* overlap extensively, so that earlier records of observer-oriented aggression by males at nests (Reilly 1970) may have been misinterpreted.

Several female territories overlapped more than one male territory. If this proves to be a typical lyrebird dispersion pattern, it is unlikely that males guarantee resources for their mates and offspring through territoriality. Male Superb Lyrebirds appear to be totally emancipated from a paternal care role.

The extent of pair bonding.—Apart from brief encounters at display mounds, an adult male typically encountered a female once daily in the breeding season, and a hen typically encountered a territorial male once in 2 days. Many such encounters involved bouts of Whisper-song courtship, but most lasted only a few minutes. Moreover, females were usually unresponsive to such courtship. Some lack of discrimination in the orientation of this male display was evident, as 93% of encountered FP groups (composed largely of immature males) elicited male courtship.

Some heterosexual contact away from display mounds was virtually inevitable,

even in the absence of pair bonding, given the spatial overlap of male and female territories. Transitory courtship during such contact has also been noted in promiscuous grouse and manakins (Kruijt et al. 1972; Lill 1974, 1976). The degree of heterosexual association was clearly far less than in many monogamous, pair-bonded species, but there are too few quantitative documentations of association levels in polygynous species to permit meaningful comparison. Clearly, however, associating with females involved only a limited time-energy investment for male lyrebirds in my study populations.

Mate selection and adult territorial dispersion.—Kenyon (1972) noted that some female lyrebirds copulated with a particular male in two or three successive seasons, but this does not necessarily prove the existence of long-term pair bonds *sensu* Hinde (1964). Lill (1974, 1976) showed that female manakins that made multiple breeding attempts in a season were mostly "faithful" to particular, promiscuous, lek-displaying males, and similar behavior occurs in the promiscuous Orange-rumped Honeyguide (*Indicator xanthonotus*) (Cronin and Sherman 1976). Moreover, the fidelity of Kenyon's hens was unknown; they might have copulated with more than one male prior to laying. The sexual protocol of Female S in this study indicates that some established hens do visit and are courted by more than one male during the pre-laying period. This observation, together with those of extra-territorial courtship excursions and female territories overlapping more than one male territory, seems more indicative of male promiscuity than pair bonding. But obviously the generality of these findings needs to be more firmly established.

The Superb Lyrebird social system parallels those of promiscuous Blue (*Dendragapus obscurus*), Ruffed (*Bonasa umbellus*), and Spruce grouse (*Canachites canadensis*) in that (a) males are widely and fairly uniformly spaced on large territories, (b) many female territories overlap several male ones, (c) hens visit more than one male before mating, and (d) heterosexual contact is largely limited to brief courtship encounters (Bendell and Elliot 1967; Gullion 1967; McDonald 1968; Brander 1967; Ellison 1971, 1973; Archibald 1975, 1976). Whether lyrebirds are really promiscuous or polygynous may never be completely resolved. In any case, avian mating systems form a graded continuum rather than falling into discrete categories, and an ecological classification is more useful than one based on how many mates one sex can acquire (Emlen and Oring 1977).

Evolutionary implications.—Strong imbalance toward females in parental investment ratios should lead both to increased variance in male mating success and a shift in the basis of mate choice by females from male parental potential to sexual competence and epigamic traits (Trivers 1972). The evolution of uniparentalism does not necessarily lead to polygamy, but it frees the emancipated sex to exploit fully any environmental potential for polygamy (Emlen and Oring 1977). Given the lack of paternal care and the small amount of time spent in heterosexual association in lyrebirds, one would predict that hens are strongly influenced in mate selection by male morphological and behavioral epigamic characters. The male mating distribution should also be highly skewed, but the stable territorial dispersion of these long-lived birds may dilute this effect somewhat, notwithstanding the occurrence of extra-territorial courtship excursions.

support, and John Alcock read and discussed the MS. I am most grateful to all these institutions and individuals for their help.

LITERATURE CITED

ARCHIBALD, H. L. 1975. Temporal patterns of spring space use by Ruffed Grouse. J. Wildl. Mgmt. 39: 472–481.

———. 1976. Spatial relationships of neighboring male Ruffed Grouse in spring. J. Wildl. Mgmt. 40: 750–760.

BENDELL, J. F., & P. W. ELLIOT. 1967. Behaviour and the regulation of numbers in blue grouse. Can. Wildl. Serv. Rep. Ser. 4.

BRANDER, R. B. 1967. Movements of female Ruffed Grouse during the mating season. Wilson Bull. 79: 28–36.

CAMPBELL, A. G. 1941. Courtship of Lyrebird. Emu 40: 357.

CHISHOLM, A. H. 1960. The romance of the Lyrebird. Melbourne, Angus and Robertson.

CRONIN, E. W., & P. W. SHERMAN. 1976. A resource-based mating system: the Orange-rumped Honeyguide. Living Bird 15: 5–32.

EDWARDS, H. V. 1919. The nesting of Lyrebirds. Emu 18: 298–299.

ELLISON, L. N. 1971. Territoriality in Alaskan Spruce Grouse. Auk 88: 652–664.

———. 1973. Seasonal social organization and movements of Spruce Grouse. Condor 75: 375–385.

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

GULLION, G. W. 1967. Selection and use of drumming sites by male Ruffed Grouse. Auk 84: 87–112.

HINDE, R. A. 1964. Pair formation. Pp. 581–582 in A new dictionary of birds (A. Landsborough Thomson, Ed.). London, Thomas Nelson.

KENYON, R. F. 1972. Polygyny among Superb Lyrebirds in Sherbrooke Forest Park, Kallista, Victoria. Emu 72: 70–76.

KRUIJT, J. P., G. J. DE VOS, & I. BOSSEMA. 1972. The arena system of Black Grouse, Lyrurus tetrix tetrix (L.) Proc. 15th Intern. Ornithol. Congr.

LEACH, J. A. 1929. The Lyrebird—Australia's wonder bird. Emu 28: 206–207.

LILL, A. 1974. Sexual behavior of the lek-forming White-bearded Manakin (Manacus manacus trinitatis Hartert). Z. Tierpsychol. 36: 1–36.

———. 1976. Lek behavior in the Golden-headed manakin, Pipra erythrocephala in Trinidad (West Indies). Adv. Ethol. Vol. 18.

MCDONALD, S. D. 1968. The courtship and territorial behaviour of Franklin's race of the Spruce Grouse. Living Bird 7: 5–25.

PAYNE, R. B., & K. PAYNE. 1977. Social organization and mating success in local song populations of Village Indigobirds, Vidua chalybeata. Z. Tierpsychol. 45: 113–173.

REILLY, P. N. 1970. Nesting of the Superb Lyrebird in Sherbrooke Forest, Victoria. Emu 70: 73–78.

ROWLEY, I. 1975. Bird Life. Sydney, Collins.

SELANDER, R. K. 1972. Sexual selection and dimorphism in birds. Pp. 136–179 in Sexual selection and the descent of man 1871–1971 (B. G. Campbell, Ed.). Chicago, Aldine.

TREGALLAS, T. H. 1921. Notes on the lyrebird. Emu 21: 95–103.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pp. 180–230 in Sexual selection and the descent of man 1871–1971 (B. G. Campbell, Ed.). Chicago, Aldine.

W. B. A. 1925. The lyrebirds of Mt. Buffalo. Emu 24: 309.

WILEY, R. H. 1974. Evolution of social organization and life history patterns among grouse (Aves: Tetraonidae). Quart. Rev. Biol. 49: 201–227.

ZIMMERMAN, J. L. 1966. Polygyny in the Dickcissel. Auk 83: 534–546.