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The relationship between ecology and the incidence of cooperative breeding in Australian birds

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Summary. Australia has many cooperatively breeding species of birds. These tend to occur in eucalypt and semi-arid woodlands rather than in rainforests or deserts. They tend to be insectivores that pursue rather than sit and wait for their prey, and tend to forage on the ground rather than above it. We propose that environments where resources do not show marked seasonal fluctuations are those in which cooperative breeding is most likely to evolve. Under these conditions birds might experience difficulty acquiring the extra food necessary to breed, especially if inexperienced. When adult survival was high, young and inexperienced birds could delay breeding. Unpredictable environments may also favor cooperative breeding, but our data do not strongly support this. Group-living would be favored further if young birds are particularly vulnerable to predators when alone. They should therefore remain in the family group and delay their dispersal until a suitable breeding vacancy becomes available. These hypotheses are not mutually exclusive, but are complementary. Both may be required to ensure that at least some year-old birds do not breed and also do not disperse. We believe that they give rise to predictions, which can be tested in future field studies.

Introduction

Cooperative or communal breeding in birds has been a topic of considerable interest to students of evolution over the last two decades. A major focus of attention has been how natural selection has favored helping behavior. A somewhat different problem is to identify whether particular ecological or demographic characteristics are associated with delayed dispersal and breeding: two prerequisites for the most common form of cooperative breeding. Do particular environments provide conditions that are particularly favorable to the evolution of cooperative breeding? Brown (1969, 1974), Koenig and Pitelka (1981), Woolfenden and Fitzpatrick (1984) and others have suggested that cooperative breeding is a feature of species in which young birds experience difficulty in finding suitable habitat in which to establish a breeding territory.

Such difficulty may occur in two types of environments. Where seasonality is low, for instance in resources such as food, adult survival may be high so that breeding vacancies are few. At the same time breeding may be difficult. In highly variable, fluctuating environments many young may be produced in good years, which in subsequent poor years are unable to find sufficient resources to breed. Both seasonality and predictability are components of stability. The use of the term stability has led to some confusion in our understanding of the types of environments in which cooperative breeding is favored. Emlen (1982a), for instance, tended to present stable and unpredictable as opposites. However, an environment can be both aseasonal and unpredictable.

Lack of seasonality in resources was considered important by Woolfenden and Fitzpatrick (1984) and Brown (1987), among others. Orians et al. (1977) found cooperative breeding more common in icterids in South America than in North America. They attributed this to the equable climate and subdued peak in food abundance in South America. Raitt and Hardy (1979) found that the Beechey jay (*Cyanocorax beechei*) was less social than its relatives living in less seasonal environments. In East Africa Zack and Ligon (1985) found that the cooperative fiscal shrike *Lanius excubitorius* experienced less seasonal variation in food supply than its non-cooperative congener *L. collaris*. In contrast Gaston (1978, 1984) and Fry (1977) have stressed that cooperative breeding occurs in seasonal environments. Gaston (1978) even suggested that cooperative breeding was rare in Sarawak rainforests because they were non-seasonal! However in the tropics and subtropics seasonality is usually expressed in terms of rainfall rather than temperature. Dry seasons do not necessarily lead to a severe food shortage in the same way that winters do in a cool temperate climate, and they do not result in greatly increased energy demand (Ridpath 1985).

With regard to unpredictability between years Brown (1980) suggested that "many communal species have irregular population fluctuations characterised by periods of slow decline alternating with rapid growth". Woolfenden and Fitzpatrick (1984), stressed the low seasonality of the Florida scrub jay's (*Aphelocoma c. coerulescens*) environment but also showed that juvenile survival varies greatly between years. Different levels of predation and marked variation in food abundance between years could both be important. If food is scarce or predators abundant young birds would do better to stay at home rather than establish their own territories and attempt to breed. Emlen and Demong (1980) indeed found that helping was more frequent in White-fronted Bee-eaters *Merops bullockoides* in years when insects were scarce. In contrast Trail (1980) found that in acorn woodpeckers (*Melanerpes formico vorus*) a population where food supply was unpredictable had fewer helpers than one where food was more predictable.

Australia has many species of cooperative breeders and many attempts have been made to explain this high incidence. Harrison (1969) proposed that the arid climate was a major factor, whereas both Thomas (1974) and Dow (1980) stressed the rather equable conditions, in particular reduced fluctuation in resources. Rowley (1968, 1976) came close to proposing our hypothesis when he suggested that the combination of irregular climate between years and lack of a severe season leads to non-dispersal of young and a variation in breeding effort between years. Dow (1980) warned that the species that breed cooperatively in Australia are very diverse in their habitat, food and behavior. He concluded that "it is most unlikely that a single ecological variable, or even a few, can be found to account for the widespread incidence of communal breeding by birds in Australia". Certainly cooperative breeding species occur in rainforests, woodlands and deserts, and among species that feed on invertebrates, vertebrates, nectar and other plant material. Dow did find some patterns in his analysis of environmental factors and cooperative breeding. The trait was most frequent in the central eastern part of the continent and least frequent in the more seasonal monsoonal far north and temperate south, and the arid center. It was also frequent in the mesic extreme southwest. With regard to climatic variables cooperative breeding surprisingly seemed to be found in regions with relatively cold winters, with out significant dry seasons and with wide seasonal variation in growth.

Predation, on nests or free-living birds, is a major cause of mortality in many cooperative breeders (e.g. Florida scrub jay *Aphelocoma c. coerulescens* – Woolfenden and Fitzpatrick 1984; green woodhoopoes *Phoeniculus purpurens* – Ligon and Ligon 1983; fiscal shrikes – Zack and Ligon 1984). Ricklefs (1980) proposed that increased detection of predators by cooperative breeders may provide an important advantage to birds that are feeding nestlings. This would be particularly true for those species with domed nests, from which visibility is limited. Many Australian cooperative breeders build domed or at least partially enclosed nests (e.g. Acanthizidae, Maluridae, *Pomatostomus*, some Meliphagidae). The Australian fairy-wrens also show a characteristic "rodent-run" distraction display at the nest, which may reduce the risk of nest-predation (Rowley 1962).

Many theoretical papers on the evolution of cooperative breeding pay more attention to food and habitat than they do to predation. Rowley (1976), Gaston (1978) and Emlen (1982a) pointed out that a critical step in the evolution of cooperative breeding is the retention of young birds in the family group until the next breeding season. Gaston further stated that a major advantage of remaining in the family group is increased detection and consequent avoidance of predators. In addition most Florida scrub jays, of any age, die through predation (Woolfenden and Fitzpatrick 1984). Delayed dispersal, which leads to larger groups, therefore could be more common in habitats where birds experience a high risk of predation or whose foraging behaviour makes them particularly vulnerable.

Over the last decade many more species have been added to the list of cooperative breeders, some of which have been studied in detail. In addition we now have extensive data on the geographic distribution of Australian birds (Blakers et al. 1984) as well as foraging data from eucalypt woodlands and forests (Recher et al. 1985; Ford et al. 1986; but also see many chapters in Keast et al. 1985).

We therefore attempt to re-analyze the frequency of cooperatively breeding species between habitats in Australia, and, for the first time, within one habitat between foraging guilds. Some patterns emerge and we discuss these in the light of the hypotheses that cooperative breeding is associated with low seasonality, high unpredictability between years and high risk of predation.

Methods

We define cooperative breeding as the situation where individuals other than two parents contribute to care of nestlings or fledglings or both. This will include species in which only a small proportion of pairs have non-breeding helpers, as well as those that typically live in groups in which more than two birds are breeding. For our analysis of cooperative breeding and habitat we have used the species listed by Dow (1980), less his first four species which are dependent on fresh-water. We have added several additional species that have subsequently been found to breed cooperatively (details in Table 1). We have chosen to work at the level of the species because congeners and even populations within a species can differ in their cooperativeness (e.g. in *Lichenostomus*, *Acanthiza* and *Climacteris*).

We have assigned these species to one or more of five habitats, in which they breed regularly (from Blakers et al. 1984). These are arranged (from mesic to xeric): rainforest (no eucalypts), eucalypt forest, eucalypt woodland (includes woodland dominated by *Melaleuca*), semi-arid woodland (mostly mallee – low eucalypt woodland, or *Acacia* – dominated woodland) and desert (either chenopod shrub-steppe or spinifex – *Triodia*). We also assigned all Australian Coraciiformes and passerines for which no evidence of cooperative breeding exists to one or more habitats. The totals were used to calculate expected numbers of species that breed cooperatively in each habitat, from the null hypothesis that the same proportions of cooperative and non-cooperative species occur in each habitat.

For comparisons involving food and foraging we chose 55 species in eucalypt woodland and forest near Armidale in northern New South Wales (30°30′ S, 151°30′ E). Species were chosen only if there were adequate data on foraging behavior (chiefly from Ford et al. 1986; Recher et al. 1985) and also on the breeding system (Table 1). More detailed studies on species that we list as non-cooperative breeders may reveal that they occasionally have helpers.

Species were separated on the basis of their major food: insects (plus other arthropods), nectar (including alternative carbohydrates like manna and honeydew), seeds, and fruit. Species for which insects were the major food (including the more insectivorous honeyeaters) were then categorized by feeding method and foraging substrate. The methods were: gleaning (perched bird takes prey from substrate), snatching (flying bird takes prey from substrate), hawking (bird leaves perch and takes prey from air), pouncing (bird drops to ground and takes prey) and pursuing (flying bird takes insects from air). Foraging substrates were: ground, bark, foliage and air.

Results

Do cooperative species differ in habitat from non-cooperative species?

Sixty-three cooperative species were classified as breeding in one or more of the five major habitats. Co-operatively breeding species are in fact most frequent, absolutely and relatively, in the intermediate habitats (Table 2). Undoubtedly part of the reason for this is that few species have been studied well in rainforest or desert. However comparative studies of thornbills (*Acanthiza*, Bell and Ford 1986) and treecreepers (*Climacteris*, Noske 1983b) show that the single species of each genus that inhabits rainforests (*A. pusilla* and *C. leucophaea*) does not breed cooperatively. In both genera, two other species that inhabit eucalypt forest and woodland are cooperative breeders (*A. reguloides* and *A. lineata*, *C. picumnus* and *C. erythrops*).

Do cooperative species consume one type of food more than others?

None of the seed-eaters found near Armidale is a cooperative breeder, nor is the single frugivore. There are no records of cooperative breeding among Australian pigeons (Columbidae, Ptilinopidae) or finches (Estrildidae) and only a single, rather doubtful record for one species of parrot (Eclectus parrot *Eclectus roratus* Rowley 1976). Pigeons, parrots and finches are the major seed-eating and frugivorous groups on the continent. The frugivorous bowerbirds are famous for their display grounds and are mostly polygynous (Marshall 1954; Borgia 1985) and none breeds cooperatively. Several honeyeaters are cooperative breeders (4 out of 9 species near Armidale), including the miners *Manorina*, which have highly complex breeding systems (Dow 1978; Clarke 1984). Interestingly most of the cooperative breeders are in the least nectarivorous genera: *Manorina*, *Melithreptus*, *Lichenostomus* (see Pyke 1980). The more nectarivorous genera (e.g. *Phylidonyris*, *Acanthorhynchus* and *Anthochaera*) do not breed cooperatively.

It is among the insectivores generally that cooperative breeders are most frequent (20 out of 49 species). They include representatives of almost all the main passerine families found in Australia (Climacteridae, Acanthizidae, Maluridae, Meliphagidae, Eopsaltriidae and Corvidae sensu Sibley and Ahlquist 1985) and both large (e.g. Australian magpie, white-winged chough) and small species (e.g. thornbills, fairy-wrens).

Do cooperative breeders use some foraging sites more than others?

The frequency of cooperative breeding among insectivores (including the less nectarivorous honeyeaters) that forage on four substrates is compared in Table 3 (basic data from Table 1). Coop-

Table 1. List of insectivorous species, occurring in eucalypt woodland and forest near Armidale, that are used in analysis of breeding system and foraging behavior. coop = cooperative breeder, non = non-cooperative breeder

Species	Breeding system	Foraging method	Foraging substrate
Laughing kookaburra *Dacelo novaeguineae*	coop	Pounce	Ground
Sacred kingfisher *Halcyon sancta*	non	Pounce	Ground
Rainbow bee-eater *Merops ornatus*	coop	Pursue	Air
Dollarbird *Eurystomus orientalis*	non	Pursue	Air
Welcome swallow *Hirundo neoxena*	non	Pursue	Air
Tree martin *Cecropis nigricans*	non	Pursue	Air
Black-faced cuckoo-shrike *Coracina novaehollandiae*	non	Snatch	Leaves
White-winged triller *Lalage sueurii*	non	Snatch	Leaves
Rose robin *Petroica rosea*	non	Snatch	Leaves
Flame robin *P. phoenicea*	non	Pounce	Ground
Scarlet robin *P. multicolor*	non[e]	Pounce	Ground
Eastern yellow robin *Eopsaltria australis*	coop	Pounce	Ground
Jacky winter *Microeca leucophaea*	non	Hawk	Air
Crested shrike-tit *Falcunculus frontatus*	coop	Glean (Tear)	Bark
Golden whistler *Pachycephala pectoralis*	non	Snatch/Glean	Leaves
Rufous whistler *P. rufiventris*	non	Snatch	Leaves
Grey shrike-thrush *Colluricincla harmonica*	non	Glean	Bark
Leaden flycatcher *Myiagra rubecula*	non	Hawk/Snatch	Air/leaves
Satin flycatcher *M. cyanoleuca*	non	Hawk/Snatch	Air/leaves
Restless flycatcher *M. inquieta*	non	Snatch	Ground/air
Rufous fantail *Rhipidura rufifrons*	non[d]	Hawk	Air
Grey fantail *R. fuliginosa*	non[d]	Hawk	Air
Willie wagtail *R. leucophrys*	non[d]	Hawk	Air
Rufous songlark *Cincloramphus mathewsi*	non	Glean	Ground
Superb fairy-wren *Malurus cyaneus*	coop	Glean	Ground

Table 1. (continued)

Species	Breeding system	Foraging method	Foraging substrate
White-browed scrub-wren *Sericornis frontalis*	coop[a,b]	Glean	Ground
Speckled warbler *S. sagittatus*	coop	Glean	Ground
White-throated gerygone *Gerygone olivacea*	non	Glean/Snatch	Leaves
Brown thornbill *Acanthiza pusilla*	non[c]	Glean	Leaves
Buff-rumped thornbill *A. reguloides*	coop[c]	Glean	Ground
Striated thornbill *A. lineata*	coop[c]	Glean	Leaves
Yellow-rumped thornbill *A. chrysorrhoa*	coop	Glean	Ground
Varied sittella *Daphoenositta chrysoptera*	coop	Glean	Bark
White-throated treecreeper *Climacteris leucophaea*	non[g]	Glean	Bark
Red-browed treecreeper *C. erythrops*	coop[g]	Glean	Bark
Brown treecreeper *C. picumnus*	coop[g]	Glean	Bark/ground
Noisy miner *Manorina melanocephala*	coop[g]	Glean	Leaves
Yellow-faced honeyeater *Lichenostomus chrysops*	non	Glean	Leaves
White-eared honeyeater *L. leucotis*	non	Glean	Bark
Yellow-tufted honeyeater *L. melanops*	coop	Glean	Leaves
Fuscous honeyeater *L. fuscus*	non	Glean	Leaves
White-plumed honeyeater *L. penicillatus*	coop	Glean	Leaves
Brown-headed honeyeater *Melithreptus brevirostris*	coop[f]	Glean	Leaves
White-naped honeyeater *M. lunatus*	coop	Glean	Leaves
Spotted pardalote *Pardalotus punctatus*	non	Glean	Leaves
Striated pardalote *P. striatus*	coop	Glean	Leaves
Silvereye *Z. lateralis*	non	Glean	Leaves
White-winged chough *Corcorax melanorhamphus*	coop	Glean	Ground
Apostlebird *Struthidea cinerea*	coop	Glean	Ground
Australian magpie-lark *Grallina cyanoleuca*	non	Glean	Ground
White-browed woodswallow *Artamus superciliosus*	non	Pursue	Air

Table 1. (continued)

Species	Breeding system	Foraging method	Foraging substrate
Dusky woodswallow *A. cyanopterus*	coop	Pursue	Air
Australian magpie *Gymnorhina tibicen*	coop	Glean	Ground
Pied currawong *Strepera graculina*	non	Glean	Leaves
Australian raven *Corvus coronoides*	non	Glean	Ground

[a] Ambrose 1985
[b] Bell 1982
[c] Bell 1983
[d] Cameron 1985
[e] Huddy 1979
[f] Noske 1983a
[g] Noske 1983b

Most other cooperatively breeding species referred to in Dow (1980) or Blakers et al. (1984)

Table 2. Numbers of cooperatively breeding species that occur in each habitat in Australia and Africa. Number of all bird species recorded for each habitat from Blakers et al. (1984). African data from Grimes (1976a)

Australia	Rainforest	Eucalypt forest	Eucalypt woodland	Semi-arid woodland	Desert
Cooperative breeders	7	35	48	36	9
Expected	23.7	32.3	37.8	26.7	14.6
All species	96	131	153	108	59

$\chi_4^2 = 20.14$ $P < 0.001$. Using total number of species to calculate expected values

Africa	Montane forest	Lowland forest	Moist woodland	Dry woodland	Desert
Cooperative breeders	2	12	20	34	3

erative breeders are better represented amongst ground foragers than among foliage or aerial foragers. The comparison among four substrates is not significant ($\chi_3^2 = 6.36$, $P = 0.10 - 0.05$) but a comparison of ground vs above ground feeding is significant ($\chi_1^2 = 4.02$, $P = 0.05 - 0.025$).

Do cooperative breeders use some foraging methods more than others?

Most cooperative breeders are gleaners whereas all snatchers or hawkers breed non-cooperatively (Table 4): a few pouncers and pursuers also breed cooperatively ($\chi_4^2 = 12.78$, $P < 0.05$). The different foraging methods can be combined into two basic strategies: the active pursuers and the more passive "sit-and-wait" predators. Cooperative species are almost entirely active pursuers ($\chi_1^2 = 9.13$, $P < 0.01$).

Discussion

The results indicate that, among Australian birds, cooperative breeders tend to inhabit eucalypt and semi-arid woodlands rather than rainforests or deserts, to be insectivores rather than gramnivores or frugivores, to forage on the ground and to glean rather than use sit-and-wait tactics. These are only general patterns, which should be regarded as tentative, as there are exceptions and clearly we still have inadequate data for many species. This proviso notwithstanding what do these trends tell us about the environmental conditions that may favor the evolution of cooperative breeding?

Table 3. Foraging sites of 55 insectivorous species according to breeding system (a few species forage often from two sites and are added 0.5 to each)

	Breeding system	
	Cooperative	Non-cooperative
Ground	10.5	6.5
Leaves	7	13
Bark	3.5	3
Air	2	9.5

Table 4. Foraging methods of 55 insectivorous species classified according to foraging method

	Breeding system	
	Cooperative	Non-cooperative
Glean	19	13
Snatch	0	7
Pounce	2	3
Hawk	0	5
Aerial pursuit	2	4
Pursue	21	17
Sit and wait	2	15

Habitat

Grimes (1976a) compared the frequency of cooperative breeders in different habitats in Africa (Table 2). He, too, found the greatest incidence in woodlands, rather than in wetter or drier habitats, though he also pointed to the lack of studies in the latter habitats. Gaston (1978) also suggested that cooperative breeders in India were most frequent in semi-arid woodland, though he did not quantify this statement. He later said that cooperative breeders generally were found in savannas in tropical and sub-tropical areas (Gaston 1984). Several North American cooperative breeders inhabit evergreen oak woodland, which superficially resembles eucalypt woodland (e.g. Mexican jay *Aphelocoma ultramarina*, Florida scrub jay, acorn woodpecker).

Does evidence exist that eucalypt and semi-arid woodlands are less seasonal in terms of food than deserts or rainforests? Studies on insects in eucalypt woodland and forests in New South Wales and Victoria (Recher et al. 1983; Woinarski and Cullen 1984; Bell 1985) and in rainforests in New South Wales (Lowman 1982) provide an answer. If we take the ratio of peak abundance to lowest abundance as a measure of seasonality the figures for eucalypt habitats range from about 3:1 to 13:1, those from rainforest from 10:1 to 20:1. Unfortunately insects were sampled using different methods; Lowman used light traps whereas the other workers sampled insects from foliage. More instructive to the comparison is Woinarski and Cullen's finding that there was a positive correlation between annual rainfall and seasonality of arthropods. Winter insects made up a smaller proportion of average insect numbers in rainforests than they did in semi-arid eucalypt woodland. Indeed several species of Australian birds move from wet forests to woodland in winter, [e.g. pied currawong (scientific names in Table 1), flame robin, rose robin and golden whistler (Blakers et al. 1984, personal observations)]. Nix (1976) used climatic variables to calculate plant growth indexes for each month throughout Australia. He found that the area west of the Great Dividing Range in New South Wales showed the least seasonality in plant growth. This coincides remarkably well with the region in which the greatest number of cooperative breeders occurs (Fig. 1).

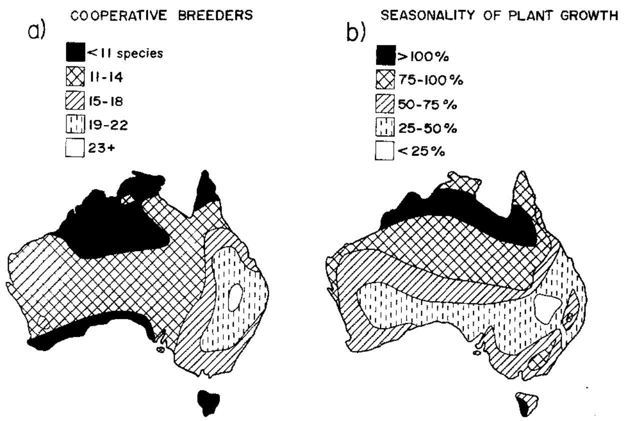

Fig. 1. **a** Distribution of cooperative breeders in Australia (from Dow 1980). **b** Coefficient of variation of seasonal growth index (from Nix 1976). Note that growth is least seasonal and cooperative breeders most frequent in inland eastern Australia. There are fewer cooperative breeders in the more seasonal north and extreme south

Is there evidence that Australian eucalypt woodlands are unpredictable? There are few data on the abundance of food in different Australian habitats over several years. However Bell's study in eucalypt woodland covered three years of increasing drought. The spring peak of insects in the third year of his study was about the same as the winter low in his first year. Clearly then some years may be very much better than others for breeding. During the last year of the drought a population of superb fairy-wrens from a nearby area made only 1.35 breeding attempts per group, whereas in the wet year after the drought they averaged 3.31 attempts (Nias 1987).

Food and foraging behaviour

Grimes (1976b), Brown (1978) and Gaston (1984) have noted previously that cooperative breeders tend to be insectivorous. Also interestingly Vogel (1985) commented that the primarily insectivorous callitrichid marmosets provide the best example of "helpers at the nest" among the non-human primates. Gaston also noted that co-operative breeders are often ground-feeders. We know of no studies that compared the foraging method of cooperative and non-cooperative species.

If lack of seasonality was a driving force in the evolution of cooperative breeding then we should predict that i) the abundances of seeds and nectar should display greater seasonality than that of insect prey; ii) in eucalypt woodland and forest the abundance of foliage, bark or aerial insects should display greater seasonality than that of ground insects; iii) pursuers should experience less seasonality in the availability of their prey than sit-and-wait predators do.

There are few data on patterns of availability of seeds, though grasses have a regular seeding cycle with a peak of abundance in summer at Walgett, 200 km W of Armidale (Wyndham 1980). Kikkawa (1980) stated that annual seed production in ungrazed pastures may be high near Armidale, but seeds are rapidly depleted. Nectar abundance has been measured at several sites (Ford 1979, 1983; Paton 1985; Pyke 1985; Ford and Pursey 1982). Locally it may fluctuate from superabundant to scarce. On a larger scale though this wide range can be dampened to some extent by birds moving between neighboring habitats with different flowering plants. Overall a period of shortage of nectar tends to occur in summer and/or autumn.

Ground invertebrates were sampled throughout the year in northern New South Wales by Cameron (1985) and Bell (1985). Their data gave peak to trough ratios of 20:1 and 12:1, which appear greater than those from foliage (3:1 to 13:1, see above) as well as those from bark (10:1 Noske 1983b) or air (6:1, Cameron 1985). These data give us no reason to believe that ground resources are less seasonal in abundance than are above-ground resources. However two species, the scarlet robin (Huddy 1979), and buff-rumped thornbill (Bell 1983) display more ground feeding in winter than in summer. These changes in behavior cannot be explained by departure of competing migrants. This suggests that ground invertebrates can be exploited more profitably in winter, relative to those from other substrates, whereas this is not true in summer. Indeed Huddy (1979), in a seven-month study, found that ground arthropods were more abundant, relative to those above ground, in the cooler months.

Sit-and-wait predators tend to take larger prey than pursuers (Ford and Harrington unpublished). Large insects tend to fluctuate more in abundance than small insects do, being particularly scarce in winter (Bell 1985). Sit-and-wait predators also tend to be migratory (11 out of 17 included in Table 1, versus 12 out of 38 of the pursuers, $\chi^2_1 = 5.3$, $P <= 0.05$). This also indicates that their resources fluctuate seasonally in abundance.

We conclude that insectivorous birds in eucalypt woodlands experience less seasonal variation in the abundance of their food than do gramnivorous birds, and there is, mostly circumstantial, evidence that ground feeders and gleaners may experience the least variation. Woinarski (1985) compared the breeding biology of Australian birds with those of North America and Europe. Insectivores in Australia have longer breeding seasons and lay smaller clutches, which can be accounted for only partly by differences in latitude from the northern continents. Woinarski attributed these differences to the low seasonality of insect abundance in Australian habitats, especially eucalypt woodlands and forests. The climate is equable, with no severe season, and the trees and shrubs are evergreen, growing through much of the year. Cooperative breeding is yet another response to a less seasonal environment. In contrast, Australian seed-eaters laid clutches that were as large as or larger than those of their northern counterparts.

Unfortunately few data exist on the variability of abundance of insects and other resources from year to year. Some evidence suggests that breeding effort of birds, at least, can vary markedly between years. Whether unpredictability of food, and other resources, between years influences the tendency to breed cooperatively can only be examined by long term studies on a variety of species.

Predation

Do inhabitants of eucalypt woodlands, insectivores, ground-feeders and pursuers experience better protection from predators by living in groups than inhabitants of rainforests or deserts, herbivores, above ground feeders and sit-and-wait predators?

The vulnerability of birds to predation and the benefits that living in groups provide in the detection and avoidance of predators will vary between habitats. Pulliam (1973) illustrated how the probability of detecting a predator increases with group size. Group-living is always better than being solitary, for detection of predators. However group living may incur disadvantages, such as greater probability of detection by a predator and more competition for food. Hence what is important is the increment in probability of detection of the predator. This is influenced by the time taken for a predator to reach a prey once the latter has detected it, which is dependent on the density of the habitat.

We suggest that habitats like eucalypt woodland or semi-arid woodlands generally are of intermediate density, and that these offer the most benefits to fledglings that remain in the family group. Put simply, birds in rainforest may have very little time to learn from others that have detected a predator, those in grassland or desert have plenty of time to detect predators themselves.

While not convincing, the only reason we can suggest for why insectivorous birds should be more vulnerable to predation than gramnivorous or nectarivorous species, is that insectivores may spend a greater proportion of their time foraging. This aspect should be explored further.

We found that ground-feeders were rather more likely to be cooperative breeders than were above-ground feeders (Table 3). Gaston (1984) also noted this pattern, and indeed many of the well-studied species outside Australia forage on open ground. Ground foragers could be more susceptible to predation than those that forage in trees and bushes, as they are vulnerable to terrestrial predators as well as aerial and arboreal ones. That the ground is a dangerous place is indicated by the fact that ground feeders usually fly up to trees when they detect predators, and almost invariably nest and roost in trees. The exceptions are cryptic species, (e.g. ground-nesting nightjars and quail). Ground foragers, if living in a group, also may be able to defend themselves better from other species that harass them. Rowley (1978) found that solitary choughs were hounded by magpies, whereas groups could withstand such attacks. Counsilman (1980) also found that groups of grey-crowned babblers experienced less interference from noisy miners than solitary birds did.

Apparently no previous attempt has been made to relate cooperative breeding to foraging method, though aerial pursuers are well represented (e.g. bee-eaters, hirundines and woodswallows). Is there any reason to believe that pursuers are more susceptible to predation than are sit-and-wait predators? We would argue yes. Gleaning birds are constantly on the move and so more obvious to predators. Also they are usually searching for and capturing prey a few mm or cm in front of them whereas snatchers, pouncers and hawkers seek prey that are usually several m away. The latter would be in better positions to detect approaching predators, and they may even be physiologically adapted to focusing better on more distant objects. Sit-and-wait foragers also tend to seek active prey and could therefore be better at detecting a moving predator. Finally hawkers and snatchers, in particular, are manoeuverable fliers and consequently may have a better chance than gleaners of escaping from a predator that has approached within striking distance. We are unsure whether aerial pursuers should be more or less vulnerable to predation than the other groups. They are safe from terrestrial and arboreal predators, but have their own specialized predators such as the hobbies, *Falco subbuteo*, *F. longipennis* (Parr 1985).

Huey and Pianka (1981) discussed predation rates on desert lizards that either forage widely or sit and wait. They suggested that the former are more vulnerable as they would encounter predators more frequently and are susceptible to both widely foraging and sit-and-wait predators. Huey and Pianka provided a few data on the horned adder, *Bitis caudalis* a sit-and-wait predator, which took a disproportionate number of widely foraging lizards.

As well as perhaps having less to gain from other group members in terms of predator detection, sit-and-wait foragers may interfere with each other while foraging together.

Conclusions

In conclusion we have observed several frequent features in the ecology of Australian cooperatively breeding birds. These can be explained by two hypotheses. First, species that experience minor fluctuations in the seasonal availability of resources would be expected to show the potential to delay breeding. Secondly, non-dispersal would be favored in species that are vulnerable to predation and, where living in groups, can significantly increase the chances of detecting predators. Once breeding and dispersal have been delayed there are strong reasons for non-breeding group members to help breeders in subsequent years (Gaston 1978; Dow 1980; Emlen 1982b).

The two hypotheses are not contradictory and most likely both factors are necessary for the evolution of cooperative breeding. In addition unpredictability between years may favor cooperative breeding, though our data neither strongly support nor refute this. Eventually, though, the occurrence of cooperative breeding will not be explained by hypothesising but only by empirically testing predictions arising from the hypotheses. Our hypotheses are testable. We suggest that studies of cooperative breeding, especially those comparing cooperative and non-cooperative species or populations of a species should attempt to assess seasonal and year-to-year changes in food availability (e.g. Zack and Ligon 1985). This could be done directly by for instance, measuring the abundance of insects on appropriate substrates or indirectly by recording the allocation of time to foraging in different seasons and years. Quantification of foraging behavior and food would be a necessary pre-requisite to such a study.

In addition a measure of the susceptibility of the species to predation should be gained. This could be done by recording the flushing distance and response of the birds to predators in the field or in the laboratory. Alternatively the relative frequency of cooperative and non-cooperative species in the diets of predators could be compared.

It is perhaps not surprising that the most cooperative of all animals, *Homo sapiens*, apparently evolved as a ground-gleaner and pursuer in semi-arid woodland and was particularly vulnerable to predation.

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