An evolutionary approach to megapode mating systems

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An evolutionary understanding of the complex mating systems of megapodes has been impaired by a historical and simplistic classification system that assumed all species to be monogamous. This approach has been challenged by behavioural ecology theories that emphasize the primacy of the individual attempt to maximize its own fitness. From this point of view the remarkable incubation techniques and the recently described behaviours of some clearly promiscuous species can be more clearly understood. In particular, the influence of the type of incubation-heat source on the mating system is paramount.

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Introduction

When Harry Frith described the mating system of the malleefowl *Leipoa ocellata* as monogamous (Frith, 1959), he was using the established classical classification of reproductive associations (e.g. Darwin, 1871): based on the number of mates obtained by each sex per breeding season, all species could be classed as either monogamous (one mate each), polygynous (more than one female per male), polyandrous (more than one male per female), or promiscuous (both sexes obtain more than one mate) (Wittenberger, 1981).

Typically, mating systems were viewed as one component of the suite of adaptations exhibited by a species, having evolved along with physiological and other behaviour characteristics. Darwin's (1871) theory of sexual selection was highly influential in drawing attention to the importance of both sexual attraction and intrasexual (especially male-male) competition in shaping mating systems.

The apparent correlation between mating system and the strength of sexual selection, with highly sexually dimorphic species usually being polygamous, appeared to emphasize the adaptative nature of such features (e.g. Orians, 1969). Thus, the high frequency of monogamy among birds (Lack, 1968) was understood as being due to either genetic pre-eminence or the ecological necessity of biparental care of young (Selander, 1965). The evolution of non-monogamous systems in birds was, therefore, seen as an adaptive solution to an unbalanced sex ratio, or an apparently inherent characteristic such as the delayed maturation of males (Selander, 1965).

There have been two major challenges to this rather deterministic concept of reproductive behaviour. First, a number of comparative studies of closely related species across different environments established that mating systems may be influenced more by ecological conditions than by phylogenetic history (e.g. Crook, 1964). Second, the general acceptance of the view that natural selection acts primarily at the level of the individual, rather than the group or species (Wilson, 1975) led to a closer examination of the behaviour of individuals. Of particular importance was the view that the principal evolutionary objective underlying the behaviour of an animal should be the maximization of its own fitness (i.e. the genetic contribution made to the next generation).

The utility of using fitness (usually computable as some measure of reproductive success (Wilson, 1975)) as a currency for evaluating individual reproductive behaviours, has reorientated interest in sexual selection, especially in relation to mate choice (see Bateson, 1983) and the conflicting interests of the sexes (see Trivers, 1972). The work of Trivers (1972) in particular, has drawn attention to the importance of parental investment by the sexes on mating patterns. For example, males and females may differ markedly in their ability (or willingness) to provide care for their young, and the fitness benefits and cost may vary substantially between the sexes. Males, with a relatively minor cost per mating, stand to gain by seeking many copulations, while females may benefit more from acquiring additional nutrients for egg, embryo or nestling development (Trivers, 1972).

The form of a species' mating system will also, however, be greatly influenced by the distribution, both spatially and temporally, of resources required for reproduction. Emlen & Oring's (1977) lucid synthesis of mating systems, ecology and fitness considerations, argued that it was the defendability of such resources (including mates themselves), and the ability of individuals to exploit this opportunity, that were of primary importance. The greater degree of control of resources by some individuals the greater the variance in reproductive success among those competeing. Moreover, the opportunity for such control will usually be largely determined by environmental factors (Wittenberger, 1981).

This view provides a more cogent and, at least in part, workable approach to understanding avian mating systems. With the great majority of birds breeding in monogamous pairs (Lack, 1968) and the opinion being that biparental care of altricial young is the primitive condition (Oring, 1982; Silver et al., 1985), much interest has centred on the influences that either maintain pairs in monogamy or that have allowed shifts away from this system (Mock, 1983).

Monogamy, in perhaps most species, appears to result from the necessity of biparental care for the young (Oring, 1982). The maximization of fitness for both parents is apparently best served by maintaining pair-bond with one mate; opportunities for extra-pair copulations may be exploited frequently (see Ford, 1983), but reproductive success is optimized by remaining with the same mate (Wittenberger, 1981), at least for the duration of the breeding season, and especially within the same territory. This socio-sexual organization may be dramatically altered in any of the following conditions:

(1) The alteration of the spatial or temporal distribution of critical resource or mates enabling monopolization by some individuals;

(2) The possibility that the young being raised are not related to the parent (normally paternal uncertainty);

(3) The potential for one parent to desert the other, provided that the deserted bird is able to successfully raise the clutch (Trivers, 1972).

Although the existence of these conditions cannot explain the evolution of all non-monogamous mating systems, they do accompany many such systems. They are of particular importance in understanding megapode mating systems.

Parental emancipation on the forest floor

Megapodes are, notwithstanding ongoing taxonomic controversy (Brom & Dekker, 1992; Sibley et al., 1988), distinctly Galliform-like in anatomy (Clark, 1964). Like other families within this cosmopolitan Order, the species are typically heavy-bodied ground birds, with a distribution suggesting a tropical origin (Jones, 1989). Galliforms nest mainly on the ground, brood relatively large clutches, and raise precocial young (Johnsgard, 1988). Typically, they are generalist feeders taking a wide variety of seeds, invertebrates and fallen fruit from the ground (Gould, 1865). Ancestral megapodes can confidently be assumed to have exhibited these features within a widespread range with moist tropical rainforests of the Australasian region (e.g. Johnsgard, 1988). The dispersal history (see Dekker, 1989) and possible evolutionary steps leading to megapode incubation methods will be dealt with elsewhere (see Dekker & Brom, 1992). Suffice it to say that the single most influential adaptive achievement of the ancestral megapodes has been their exploitation of external sources of heat for the incubation of eggs (Clark, 1964; Jones, 1989). The evolutionary implications of this have been revolutionary and have shaped virtually all aspects of megapode ecology and behaviour. The most important of these are discussed briefly here.

(i) The end of the 'clutch'

Almost all birds (some brood parasites are exceptions; Oring (1982)) produce eggs in temporal bundles: typically individual eggs are layed at regular intervals until a set clutch size is reached whereupon brooding commences. Although the actual number of eggs, the intervals between laying, and the capacity of females to replace loss of eggs or clutches may vary greatly among species and populations (Lack, 1968), clutch size is subject to powerful selection pressures and constraints (Murphy & Haukioja, 1986). In general, all species should seek to produce the largest number of offspring that can be successfully brooded and raised to independence. The actual size of a clutch, then, will be a trade-off between nutritional and energetic condition, life history traits, and individual parental tactics (Wilson, 1975).

Through having their eggs incubated by a source of warmth external to themselves, megapodes have freed themselves from the costs associated with brooding, parental care, (including the protection and nurture of young), and any indirect opportunity costs related to lost time associated with parental duties (Wittenberger, 1981). Critically, this has allowed them to evade the main constraints to clutch size, and thereby greatly increase potential fecundity by allowing the possibility of a more sustained production of eggs. This was facilitated by a predetermined propensity for indeterminate egg laying (a gallinaceous trait). Thus, the route to greater reproductive success was markedly simplified; females could concentrate on nutrient and energy accumulation, while males could concentrate on methods for appropriating this reproductive potential. While the response of females has apparently been the same in all environments (maximized foraging), the approach of males has depended largely on the type of incubation source used (see below).

(ii) The end of direct parental care

Most birds ensure the synchrony of hatching of their chicks by commencing brooding only when the clutch is complete (Lack, 1968). Megapodes, however, lose this facility completely by laying eggs in pre-heated incubation sites where each egg begins to develop immediately after laying (Clark, 1964). Hatchlings will, therefore, emerge from the incubation site at intervals throughout the prolonged period (5 - 8 months, Jones, 1989) of mound function. This negates the possibility of gathering hatchlings together and leads to selection for highly precocial chicks. Indeed, megapodes produces the most precocial chicks of all birds (Nice, 1962), with the ability to thermoregulate, feed, run and evade predators being evident immediately upon emergence (Jones, 1989). The extreme precociality correlates with the high yolk contents (Dekker & Brom, 1990) and the large size of megapodes eggs (3.5 times larger than expected for other Galliformes (Seymour & Rahn, 1978), and is indicative of the great energetic investment made by females in their eggs (Clark, 1964).

(iii) Male control: incubation site or mate?

The crucial emancipation of females from parental duties appears to have occurred independently of males. The evolution of the use of external sources of heat for incubation probably started with the covering of eggs with leaf litter in the hot, moist tropics (Dekker & Brom, 1992; Frith, 1959). Males theoretically faced a major 'choice' of reproductive strategy, given that female fecundity depended upon sustained foraging (assuming that the rainforest floor was a rich and relatively homogenous source of foods): whether to remain with the female in order to monopolize her reproductive output, or remain at the incubation site in order to maximize contact with females coming to lay. The form of the mating system now exhibited by different species in different environments will have resulted largely from the influence of the spatial and temporal availability of the incubation source used, and the ability of males to exploit that opportunity (Emlen & Oring, 1977).

Another look at megapode mating systems

Until recently, megapodes were regarded, implicitly, as being universally monogamous (e.g. Frith, 1956; Baltin, 1969; Crome & Brown, 1979) and with apparently compelling evidence. Most species appeared to maintain close and permanent pair bonds, and many demonstrated numerous characteristics often correlated with prolonged monogamy: duetting, highly synchronised behaviour, and monomorphism (Ripley, 1964; Crome & Brown, 1979). The major divergence of breeding behaviour within the family is related to the amount of time paired individuals spent apart: in some species, typified by those using permanent heat sources, mated birds never separated, while in others, typically mound-builders, males remained at the mound while females foraged far from the site (Jones, 1989). Despite the possibility of these females meeting and mating with other males, males tended and maintained their mounds for prolonged periods. Based on Frith's (1962) detailed study of the immense labour of the male malleefowl, and their own behavioural observations, Immelmann & Böhner (1984) concluded that such an investment by males would only be likely in a strictly monogamous system. By equating mound work with parental care, these authors extended the argument that extensive paternal care should occur only with high paternal certainty (Trivers, 1972) to all mound-building megapodes (Immelmann & Böhner, 1984). Thus, both of these two groupings of megapodes appeared to exhibit monogamy for sound theoretical reasons. The principal exception was that of the mound-builders known as brush-turkeys, the only megapodes exhibiting clear, if seasonal, sexual dimorphism (see Coates, 1985). Nonetheless, captive studies appeared to support monogamy in one species, the Australian brush-turkey *Alectura lathami* (Baltin, 1969).

It has been the result of the first detailed field studies of the reproductive behaviour of Australian brush-turkeys (Jones, 1987) that has lead to a reassessment of the classification of mating systems of megapode species. Of crucial importance has been the description of widespread promiscuity of both sexes, as well as the absence of evidence of pair bonding (Jones, 1990a). Moreover, males continue to tend mounds that almost certainly contain eggs fertilized by other males (Jones, 1990b). It is likely that these findings are not peculiar to a particular population but also parallel other brush-turkey species in Papua New Guinea (Coates, 1985; Kloska & Nicolai, 1988).

There are two main challenges associated with these results that must now be addressed: (1) an explanation of the apparent violation of cuckoldry avoidance evident in male mound-tending despite low paternal certainty (Maynard Smith, 1984); and (2) the necessity to re-examine the mating systems of other megapodes in this light.

Mounds are multifunctional

While it is obvious that mounds are constructed and maintained for the incubation of eggs (Frith, 1957; Jones, 1988a), this feature also ensures that the structure serves another crucial function: attracting females. Among the mound-building megapodes, mounds are the only site of incubation and are therefore an essential reproductive resource. The relative success of a particular male in attracting females will depend in part on the number of alternative sites available to laying females (Jones, 1990b). The intense interaction of male brush-turkeys over mound ownership can be interpreted as attempts by some individuals to control the number of alternative mounds (Jones, 1990b). Indeed, the males most successful in receiving eggs are those maintaining the most mounds for the longest duration (Jones, 1990b).

However, the high rate of promiscuous meetings observed in Australian brush-turkeys mean that many eggs may have been fertilized by other males. This is especially likely in dense populations where females are able to encounter many males (Jones, 1988a), but it is always a possibility wherever males cannot or do not remain continuously with females. Therefore, all males of species where mounds rather than females are guarded, tend their mounds and incubate eggs despite some degree of paternal uncertainty. It is regarded as axiomatic that males should avoid expending time and energy in raising young not their own (Maynard Smith, 1984). A solution to this apparent contradiction of theory may lie in a re-examination of the function and functioning of incubation mounds (Jones, 1989).

First, the principal cost of cuckoldry is associated with a reduction of the males' overall potential reproductive success (Ridley, 1978). This cost, however, is incurred only where the form of parental care cannot be shared among offspring (Wittenberger, 1981). In megapodes, however, the main form of paternal care expended is the work associated with providing the incubation site (Jones, 1990b). This form of parental care is fully shareable; the addition of new eggs (within some constraints associated with the oxygen demand of embryos; see Vleck et al., 1984) does not deplete the quality of care received by any of the other eggs within the mound.

Second, because females will (presumably) deposit their eggs only in functioning, adequately maintained, and appropriately constructed mounds (Frith, 1957; Jones, 1988b), males will be obliged to ensure that the necessary incubation conditions are available. Because a males' presumed reproductive success will depend (at least in part) on the number of times females return to his mound to lay and copulate, his best tactic is to maintain a suitable mound for as long as possible. Although the problematic issue of female choice has yet to be resolved in Australian brush-turkeys (Jones, 1990b), it is highly likely that males are selected to some extent on their mound provision abilities. This appears to be an evolutionarily stable strategy (Maynard Smith, 1984): neither males nor females appear able to improve their reproductive success by adopting alternative activities. There are, however, numerous *tactics* that individuals may employ to improve their probability of success. For example, male Australian brush-turkeys compete for mounds and may seek to expel or usurp other males, or maintain two mounds simultaneously (Jones, 1990b). Some males, apparently moundless individuals, also appear to be trying to sneak copulations by occupying functioning mounds during absences by the owner (Jones, 1990a). This highly conditional tactic remains to be evaluated but has not been observed to have been successful to date (Jones, 1987).

In summary, mound-tending by males allows them to provide the conditions necessary for both the successful incubation of eggs, and attracting visits by laying females. The form of this investment by males also minimizes the costs of cuckoldry should it occur. The risk of cuckoldry will remain wherever females are not guarded but can be offset by males maximizing the probability of fertilization following each copulation. The disruptive behaviour of male Australian brush-turkeys toward laying females has been interpreted as an attempt to stall the passage of the imminent egg long enough to allow the sperm to reach the sperm storage organs (Jones, 1990a). The efficacy of this behaviour will depend on the extent and promptness that females facilitate sperm competition through promiscuous matings.

Three types of Megapode mating system

Much of the preceding discussion has centred on one species, the Australian brush-turkey. This is due to its prominence as a non-monogamous megapode that has been closely studied. It is, however, a representative of only one of three major types of mating systems that have been discerned. A brief description of those follows, with some comment on the reproductive strategies of the sexes that is evident.

Type 1. Female-defence monogamy

As described above, one of the most crucial consequences of the external sources of heat by megapodes was the reorientation of female investment from parental care to fecundity. This would be best served by unrestricted foraging for the maximum period possible. Yearly egg production will then depend on the optimal trade-off between egg size and number (and associated degree of embryonic development), and nutritional and energetic balance (Seymour, 1985).

In order to obtain maximum benefits from this fecundity, males need to ensure that all of the eggs produced are their own. In most species of bird, females are fertile for a specific period extending from just before the start of egg laying until the clutch is completed. By guarding their mates throughout this period, males can protect their paternity (Lumpkin, 1983). In megapodes, the prolonged period of egg production means that the fertile phase may extend for many months (Frith, 1956; Jones, 1988b). Only in species that utilize the more or less permanent sources of heat that require little or no maintenance (i.e. geothermal areas, beaches, or non-defended mounds), would males be able to remain with females permanently.

This type of mating system appears to be exhibited by all of the *Megapodius* species (including the mould-building species) (Crome & Brown, 1979; Coates, 1985) and *Macrocephalon* (Dekker, pers. comm.; Mackinnon, 1978). The little known *Talegalla* species are also placed in this group, although confirmation by field observations are needed (Coates, 1985).

Type 2. Resource-defence polygyny plus polyandry

Where megapodes must provide incubation sites by the laborious investment of time and energy in siting, constructing and maintaining a mound (Frith, 1962; Jones, 1988b) males are predisposed to defending this structure from other males that may seek to expel or usurp the constructor (Jones, 1990b). These males are therefore forced to lose control of their paternal certainty, and therefore compete, albeit indirectly, for the available females. Such species show evidence of sexual selection: males are larger, and most exhibit features possibly associated with male-male communication of status or mate attraction (Jones, 1989). These species exhibit seasonal heightened neck and head colouration, and the development of inflatable neck and head sacs (see Coates, 1985).

While *Alectura* is the type-source for this form of mating system, field and captive studies of *Aepypodius* species (Coates, 1985; Kloska & Nicolai, 1988) have indicated many important similarities between these genera.

Type 3. Resource-defence monogamy

In many ways, this type of mating system, unique among the megapodes, is the least representative of the array of mating systems exhibited by the family. It is exhibited solely by the malleefowl, a species confined to extremely arid environments. Although showing many attributes of a permanently monogamous species (see Frith, 1962; Böhner & Immelmann, 1987), its social organization is nonetheless very similar to that of the promiscuous brush-turkeys, with mated birds spending little time together as a result of the necessities of foraging for females and mound tending by males (Frith, 1962). While, theoretically, this leads to a reduced paternal certainty, this may be of little consequence to this species. First, the costs of some cuckoldry may not be serious among mound-builders (Jones, 1990a). Second, the ecological imperatives of the malleefowl's environment suggest that their strategy is a 'best available option'. The aridity of its range also predicts that population density of such large birds will be relatively low, imposing small probabilities on encounter rates with other birds. However, radio-tracking of malleefowl in South Australia (Booth, 1987) has indicated that female home-ranges may include other active mounds, therefore allowing for the possibility of extra-pair copulations (see Jones, 1989). While males would be expected to exploit such opportunities, it is uncertain whether females would seek additional fertilizations, although there are sound theoretical reasons to expect this (Fitch & Shugart, 1984). Notably, the first confirmed incidence of non-monogamy in this species has recently been reported (Weathers et al., 1990). In this case, a single male maintained pair-bonds with two females by tending simultaneous mounds. This parallels the mound-ownership tactics of Australian brush-turkeys (Jones, 1990b) and suggests that the two types of mating system may reflect similar reproductive tactics by males in both species. It is highly probable that the close pair-bonding evident among malleefowl (the principal contrast with the type 2 system), is an adaptation to ecological conditions providing the best strategy for the prolonged interactions necessary for successful reproduction in certain habitats, including arid areas (Ford, 1989).

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